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Seasonal Distribution of Cod (*Gadus morhua* L.) Along the Canadian Atlantic Coast in Relation to Water Temperature[1,2]

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ABSTRACT

Seasonal relationships between size, bottom temperature, and distribution of cod are described for the western Gulf of St. Lawrence and Nova Scotia Banks.

In summer, in the western Gulf of St. Lawrence, cod are distributed from 35 to 145 m at bottom temperatures from –0° to 6°C. They are most abundant at about 100 m where the temperature is around 1°C. In winter they are concentrated in 130–180 m along the western slope of the Laurentian Channel at bottom temperatures from 1° to 3°C.

On the Nova Scotia Banks cod are less abundant than in the Gulf of St. Lawrence. They are found mainly around Banquereau, Middle Ground, and the northern edges of Sable Island Bank. Further to the west cod are replaced by haddock as the dominant species. Nova Scotia Banks cod are found in shallower and warmer waters than Gulf cod, both in summer and winter. In summer they are present from 65 to 110 m at bottom temperatures varying from about 1° to 8°C. In winter they are taken primarily at 90–135 m at bottom temperatures from 2° to 4°C.

Area and depth distributions of commercial catches reflect the seasonal pattern of cod migrations and distributions demonstrated in surveys and tagging studies.

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[2]Contribution No. A-7, ICNAF Environmental Symposium, Rome, 27 January–1 February, 1964.

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INTRODUCTION

MOST GROUNDFISH species undergo seasonal changes in horizontal and vertical distribution. These changes have direct effects on the fishery and many are known by commercial fishermen.

In summer, cod taken commercially and recorded from ICNAF (International Commission for the Northwest Atlantic Fisheries) Divisions 4T and 4V are caught mainly in shallower water off Gaspé and in Chaleur Bay. But in winter this stock is no longer present in the Gulf of St. Lawrence. It has moved southwest into deep water along the Laurentian Channel mainly to Division 4Vn, or even as far south as Banquereau (4Vs).

On the north and east sides of the Laurentian Channel (Divisions 4R and 4S, Fig. 1) cod are also found in shallow water, mainly in Division 4S in summer and autumn. In late autumn they migrate into deep water and southward and even outside the Gulf of St. Lawrence. As a result, they are caught in deep

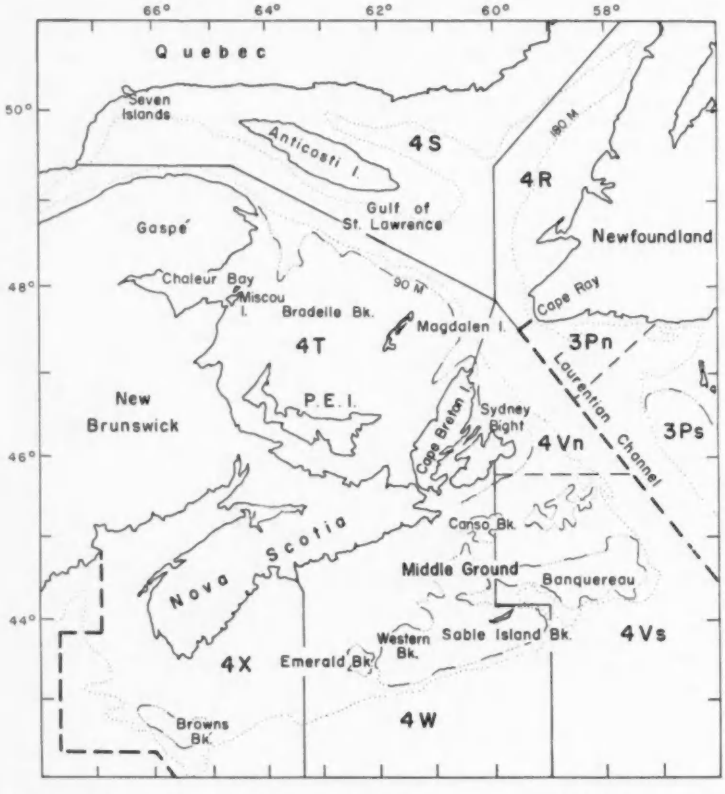


FIG. 1. Map of ICNAF Subarea 4 (including 3Pn and part of 3Ps) showing localities mentioned in the text.

water in the southern part of 4R and the northern part of 3P in late winter and early spring.

Offshore Nova Scotia Banks cod (Division 4W) show less extensive horizontal migrations. All stocks, however, are found in shoaler water and on top of the banks in summer and in deep water in winter.

The horizontal and vertical migrations of Subarea 4 cod are generally well known through previous taggings carried out both in summer and in winter (McKenzie, 1956; McCracken, 1959; Templeman and Fleming, 1962; Martin and Jean, 1964). Seasonal migrations are also shown by catch records kept by some skippers of the Canadian mobile fleet. However, it was not until 1957, when systematic research-vessel surveys in Subarea 4 were started, that the seasonal changes in the environment of cod were studied throughout the year and related to these migrations.

The present paper demonstrates the extent of the seasonal migrations of cod from records of research-vessel surveys, from distribution of the otter-trawl fleet, and from recaptures of tagged fish. It also describes changes in the environment, mainly temperature, which bring about or accompany these migrations. Finally, the effects of short-term hydrographic variations on cod distribution are discussed.

MATERIALS AND METHODS

This study is based on research-vessel surveys conducted from 1957 to 1962. The area covered extended from Cape Gaspé (4T) southward to Banquereau (4Vs) and Emerald Bank (4W) (Fig. 1). Three different vessels were used at various times during this period. Their main characteristics and details of gear used are listed in Table I.

Cod catches by the *Harengus* and *J. J. Cowie* were compared by fishing these vessels together off Miscou in the summer of 1960. Later in the same year, *Harengus* and *A. T. Cameron* catches were compared by fishing together in the western Gulf of St. Lawrence. On the average, the *Harengus* caught 2.1 times as many cod as the *J. J. Cowie*, and the *A. T. Cameron* outfished the *Harengus* by a ratio of about 1.5 to 1 for cod. For comparability, therefore, all cod catches were adjusted to those of the *Harengus* by multiplying *J. J. Cowie* catches by a factor of 2.1, and those of the *A. T. Cameron* by a factor of 0.66.

All survey tows were made using a fine-mesh codend cover or liner (25–38 mm) (Table I).

Whenever possible, all cod taken were measured. This was done with only a few exceptions in surveys carried out by the *J. J. Cowie* and *Harengus*. However, this was impossible for *A. T. Cameron* catches that exceeded 30 baskets (about 1200 kg). In this case, the sampling procedure used was generally as follows: all the largest cod (80 cm or larger) were measured. Medium-size cod were then placed in baskets and 1 basket out of 2, 5 or 10, etc., (depending on the size of the catch and the time available) was picked at random for measurement. Finally, fish smaller than about 30 cm were thoroughly mixed in basket lots and a sample was drawn. The limitations of random basket-lot sampling have been discussed by Paloheimo and Dickie (1963). Since whole catches were generally

TABLE I. Characteristics of the research vessels and gear used during groundfish surveys off the Atlantic coast of the Canadian mainland, 1957–62.

Period & season	Summer 1957–58	Summer 1959–62	Winter 1959–62
Research vessel	*J. J. Cowie*	*Harengus*	*A. T. Cameron*
Length (overall), *m*	21.2	25.6	53.2
H.P.	100	270	1000
Tonnage (registered)	49	109	753
Trawl:			
Headrope length, *m*	11.6	18.3	24.0
Rollers	Rubber on bosom Disks on wings	Rubber on bosom Disks on wings	Rubber throughout
Material	Cotton	Manila	Manila
Mesh size, *mm*	124–82	114–108	124–76
Codend:			
Material	Nylon	Various synthetic fibres	Manila
Mesh size, *mm*	102–114	114–121	76
Auxiliary equipment	38-mm cover	25-mm cover 30-mm liner (after 1960)	30-mm liner
Towing speed, *knots*	2.5	3.0	3.9
Duration of tow, *min*	45	30	30

measured, the inaccuracies which may have resulted from random basket samplings are not considered important.

All three vessels listed in Table I were equipped with echo sounders. These instruments were used extensively during all cruises to indicate the presence or absence of fish. Special echo-sounder surveys to augment observations on distribution obtained by trawling were conducted mainly by the *A. T. Cameron* during winter cruises. Surface and bottom temperatures were taken and a BT cast was made at each fishing station. Surface and bottom sea water samples for salinity determinations were also collected at most survey stations.

COD STOCKS OF THE WESTERN GULF OF ST. LAWRENCE AND OFFSHORE NOVA SCOTIA BANKS

Fish "stocks" are more or less well-defined groups of individuals with recognizable morphological or physiological characters. Stocks generally do not mix, or if they do, it is only on a limited scale. The term is often used interchangeably with "population". Templeman (1962), however, distinguishes between population and stock. In his terminology, "population" refers to "the cod occupying any defined area at a particular time", and "stock" refers to a group of fish exhibiting unity of certain characters within itself and little mingling with other groups. The term "population" is avoided in the present paper and "stock" is used in the sense defined above.

Cod along the Atlantic coast of the Canadian mainland are divided into several more or less discrete units, both offshore and inshore. From vertebral

counts, McKenzie and Smith (1955) recognized four stocks in the southwestern Gulf of St. Lawrence, three on the offshore Nova Scotia Banks and at least four along the inshore Nova Scotia coast. West of the Laurentian Channel the Gulf of St. Lawrence stocks are: Cape Breton, Prince Edward Island, Chaleur Bay, and Gaspé. To these, Templeman (1962) adds a Magdalen Islands stock which he considers "doubtful". Results of summer (McCracken, 1959) and recent winter taggings (Martin and Jean, 1964) show, however, that these stocks mix in winter along the western edge of the Laurentian Channel off Cape Breton. Templeman (1962) refers to the whole as a "Gulf of St. Lawrence super-stock". In the present discussion, cod from the southwestern Gulf (4T–4Vn) are considered as one unit or stock.

Recent taggings (Marcotte, unpublished; Jean, 1963) northeast of the Laurentian Channel on the north shore of the Gulf of St. Lawrence (4S) indicate that cod found as far west as Seven Islands in summer join the west coast of Newfoundland stock (Templeman and Fleming, 1962) and are caught in the Cape Ray area (4R and 3Pn) of Newfoundland in early spring.

Cod southwest and northeast of the Laurentian Channel were believed to make up more or less discrete units. However, Jean (1963) showed that they are not as independent as was originally thought. Of the first-year returns from Jean's October 1961 tagging at Seven Islands, about 20% crossed the Laurentian Channel and were caught in the southwestern Gulf the following summer. The rest of the recaptures were made along the north shore of the Gulf of St. Lawrence (4S) during that summer and autumn.

The offshore Nova Scotia Banks stocks identified by McKenzie and Smith (1955) are: Banquereau, Sable Island and western Nova Scotia (Browns Bank).

Several inshore Nova Scotia stocks have been defined either from taggings (McCracken, 1956; McKenzie, 1956) or from vertebral counts (McKenzie and Smith, 1955). They are independent from the offshore stocks. The present paper, however, is concerned only with offshore stocks.

The Gulf of St. Lawrence stocks, southwest and northeast of the Laurentian Channel, are essentially migratory. They move south in late fall and are found outside the Gulf (on each side of the Laurentian Channel) in late winter and early spring (McCracken, 1959; Templeman and Fleming, 1962; Marcotte, unpublished; Jean, 1963). Winter taggings (Martin and Jean, 1964) have shown that cod found off the east coast of Cape Breton, and even as far south as the southeastern peak of Banquereau in winter return to the Gulf of St. Lawrence in spring and summer.

In contrast, the offshore Nova Scotia Banks cod stocks are less migratory. Spring and summer taggings (McKenzie, 1956) as well as winter taggings (Martin and Jean, 1964) of Sable Island and Banquereau stocks show limited northeasterly movements in spring and westerly movements in late fall. Similarly, the Browns Bank stock (Jensen, unpublished) exhibits limited movements and a slight degree of mixing with the eastern Georges Bank stock.

This paper deals with only three of the above-mentioned stocks: the southwestern Gulf, the Banquereau, and the Sable Island Bank stocks.

SEASONAL CHANGES IN DISTRIBUTION OF COD IN RELATION TO WATER TEMPERATURE

Horizontal Distribution

The seasonal changes in horizontal distribution of Subarea 4 cod are reflected in catches by both research and commercial vessels.

Research-vessel surveys

The 1960 research-vessel catches show better than those of other years the seasonal variations in horizontal distribution of cod in Subarea 4 because a more extensive area was studied. The area covered in winter (January–March) and summer (May–July) extended from Cape Gaspé south and southwest to Emerald Bank (Fig. 1). Essentially the same fishing stations were covered during both winter and summer surveys.

The average catch per tow of small (38 cm and smaller), medium (39–68 cm), and large (69 cm and larger) cod caught in the 1960 winter and summer surveys is shown in Fig. 2.

Winter distribution. Cod increased in size and number from Gaspé to southeastern Cape Breton, and also from shallow to deep water. A few very small fish of the 0- and 1-year group (smaller than 22 cm in length) were caught off Miscou Island in 35–55 m. Only fish of this size were caught around Miscou Island. In deeper water off Gaspé and north of Magdalen Islands (Fig. 2) slightly larger fish (up to 38 cm) were caught in increasing numbers as one moved from shallow to deep water and from north to south. Medium-size cod (39–68 cm) were caught in small numbers and in deep water off Gaspé. The number of medium-size cod increased southward, becoming greatest off Cape North and Sydney Bight in the Cape Breton Island area. Large cod (69 cm and larger) were not found in large proportion in the survey catches. They were present mainly in the Cape Breton area. Catches of all sizes of cod decreased again as one moved southwestward along the southern Cape Breton coast toward Canso Bank.

In the Banquereau area, most easterly of the offshore banks, catches were generally smaller than off Cape Breton. Sizes of fish caught were similar to those caught off Cape Breton, with perhaps a greater representation of the larger sizes.

To the westward, catches of cod on Middle Ground, Sable Island and Emerald Banks were even lighter than on Banquereau and included more large fish than those on Banquereau and off Cape Breton.

The 1960 winter surveys confirm the results of taggings. Both show that most of the commercial-size cod (39 cm and larger) leave the Gaspé sector of the Gulf and move south toward the Cape Breton area in winter. Once they are out of the Gulf, cod do not seem to migrate in any quantity westward toward Canso Bank. Although large quantities may be caught in the deeper water southeast of Cape Breton, their numbers decrease rapidly westward and are almost nil in the Canso Bank area. These observations were confirmed by an extensive echo-sounder survey of this area in early spring of 1963 (Jean, unpublished data).

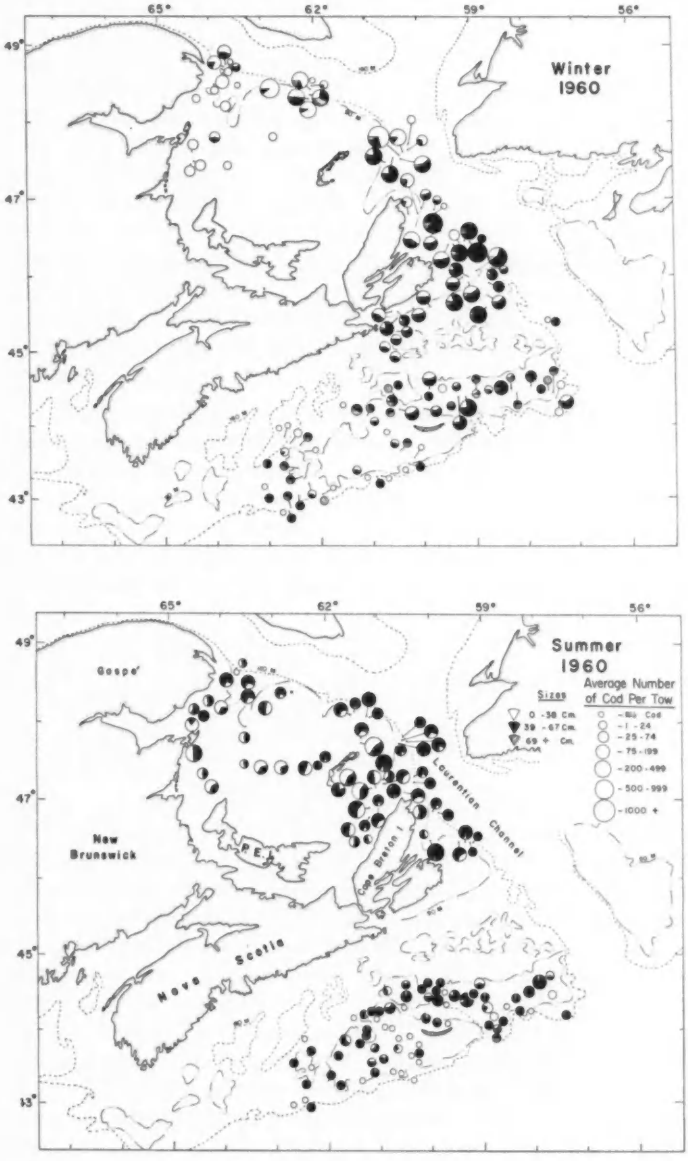


FIG. 2. Distribution of cod catches by research vessels along the Canadian mainland in winter and summer of 1960.

The winter distribution of cod size categories, shown in Fig. 2, suggests that Gulf cod migrate south as far as the southern edge of Banquereau. Winter taggings have confirmed this. A few of the cod tagged on the southern edge of Banquereau in winter 1959 returned to the Gulf in summer (Martin and Jean, 1964).

Cod caught southwest of Banquereau, i.e. on Sable Island and Emerald Banks, differed in size composition and in abundance from those of the Cape Breton area. This suggests that the Sable-Emerald stock is discrete from that found north of Banquereau. Winter taggings (Martin and Jean, 1964) have shown that this is the case.

SUMMER DISTRIBUTION. Surveys in late spring and summer of 1960 (Fig. 2) showed that cod of commercial sizes had returned to the Gulf of St. Lawrence. They were present off Miscou and Gaspé in intermediate depths where they had been absent in winter. Furthermore, both small- and medium-size cod had moved into shallow water in these areas and around the Magdalen Islands. Catches were light in Sydney Bight although they had been heavy in winter.

On the offshore Nova Scotia Banks (Fig. 2) summer catches were mainly on top of the banks. Cod were generally more abundant in the Banquereau area, less abundant on Western and Sable Island Banks and still less numerous on Emerald Bank.

The study of winter and summer horizontal distribution of cod (Fig. 2) shows the migratory characteristics of these stocks. The conclusions are supported by recent taggings which demonstrate that Gulf of St. Lawrence cod are essentially migratory (McCracken, 1959; Martin and Jean, 1964). They move in deep water along the Laurentian Channel and southeast mainly out of the Gulf. They return to shoaler water and into the Gulf in spring. Offshore Nova Scotia Banks cod (Western and Emerald Banks), on the other hand, are less migratory (McKenzie, 1956; Martin and Jean, 1964) than Gulf cod.

COMMERCIAL FISHERY

The seasonal changes in horizontal distributon of cod shown in research-vessel surveys are reflected in the otter-trawl fishery in Subarea 4. Location of cod catches from Gaspé to Emerald Bank (Divisions 4T, V and W) as given by log records of Canadian otter trawlers in 1959 is presented by quarter in Fig. 3. Those for the year 1959 are used here instead of those for 1960 because analysis of 1960 log records was incomplete at the time of writing. As changes in fishing practices from one year to the next are generally small, the 1959 data are taken as representative.

From January to April, southwestern Gulf of St. Lawrence catches (Fig. 3) came from the northwest coast of Cape Breton Island. They were made almost entirely in January because, later on, ice prevented fishing in that area. From May to July, Gulf catches were about equally divided between the west coast of Cape Breton and the Gaspé coast (Fig. 3). However, catches off Cape Breton were made early, mainly in May, whereas those off Gaspé came later, in June and July. From August to October, catches came from the Gaspé and northern

New Brunswick areas. Finally, in November and December, the Gulf otter-trawl fishery had shifted south again to the northern end of Cape Breton and even beyond the Gulf to the eastern shore of Cape Breton (Fig. 3).

Similar seasonal changes, although more limited in extent, were observed on the offshore Nova Scotia Banks (Fig. 3). First-quarter catches came from deep water along the edges of Banquereau, Western Bank, and from the channel between Western and Emerald Banks. During the second and third quarters the fishery shifted to the eastward and to shoaler water, especially on Banquereau. Finally, in the fourth quarter, the fishery moved back to the westward and to the edges of the banks. The seasonal changes in distribution of the cod fishery on the offshore Nova Scotia Banks agree with the results of research-vessel surveys and winter taggings (Martin and Jean, 1964).

To summarize, the fishery for offshore Nova Scotia Banks cod moves eastward and into shallow water in summer and returns westward into deeper water in winter.

Vertical Distribution

As in the study of horizontal distribution, survey data on seasonal changes in vertical distribution of cod in Subarea 4 were supplemented by data derived from commercial fishing operations. However, depth entries in log records of commercial catches were not precise enough for a study of vertical distribution. We have used instead data on returns of tags released in Subarea 4 since 1955 and subsequently recovered during commercial fishing operations.

Gulf of St. Lawrence and Cape Breton Surveys

Research-vessel surveys were conducted in the southwestern Gulf since 1957. For reasons already given, the 1960 surveys were arbitrarily chosen to show the relationship between water temperatures and vertical distribution of cod. In 1960, three sets of cruises were made in the Gulf and in the Cape Breton area in winter (January), spring (May), and autumn (October).

Winter. Ice conditions were not as severe as usual in the Gulf of St. Lawrence in January 1960 (Black, 1960), and the first January survey of groundfish ever made with a research vessel was carried out along the western edge of the Laurentian Channel from Cape Gaspé south to the east coast of Cape Breton. Four fishing sections from shallow to deep water were made along the Laurentian Channel. The first and most northerly section extended from the mouth of Chaleur Bay northeast to Cape Gaspé. The second and third sections were made north and east of the Magdalen Islands. The fourth and most southerly section cut across Sydney Bight off the east coast of Cape Breton.

The size compositions of cod caught at various depths in each section are shown in Fig. 4 along with profiles of the bottom and the distribution of isotherms.

In the Gaspé section catches were relatively light at all depths fished. In the shallowest water (30 m and less), only a few very small fish (10–13 cm) were caught. Bottom temperatures at these depths were close to freezing point (–1.5°C). At greater depths (35–120 m) and at temperatures lower than –1.0°C, the catches were also light and the fish small (14–22 cm). Slightly larger quan-

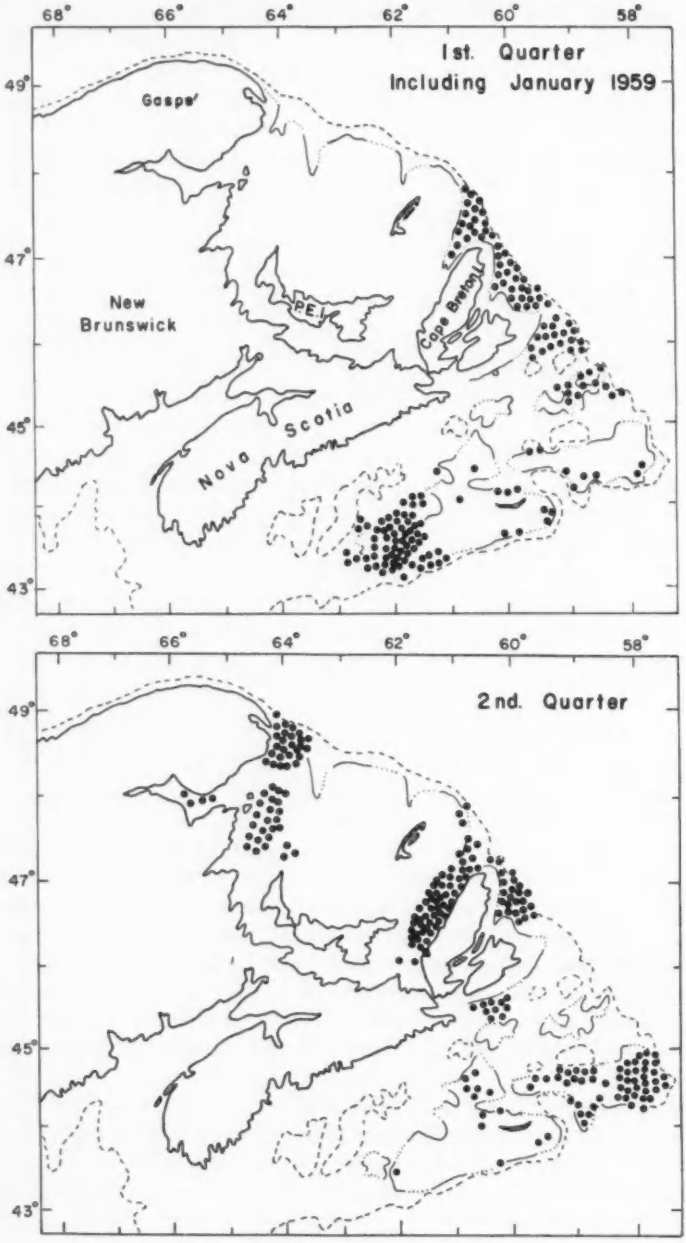
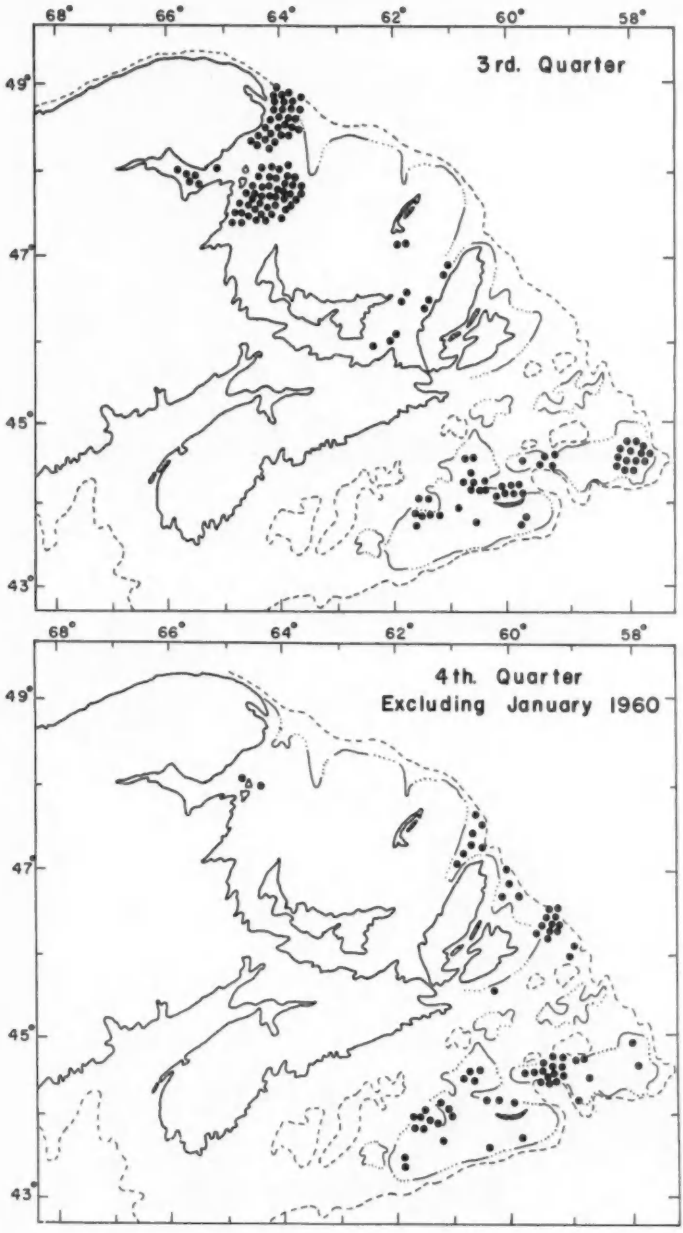
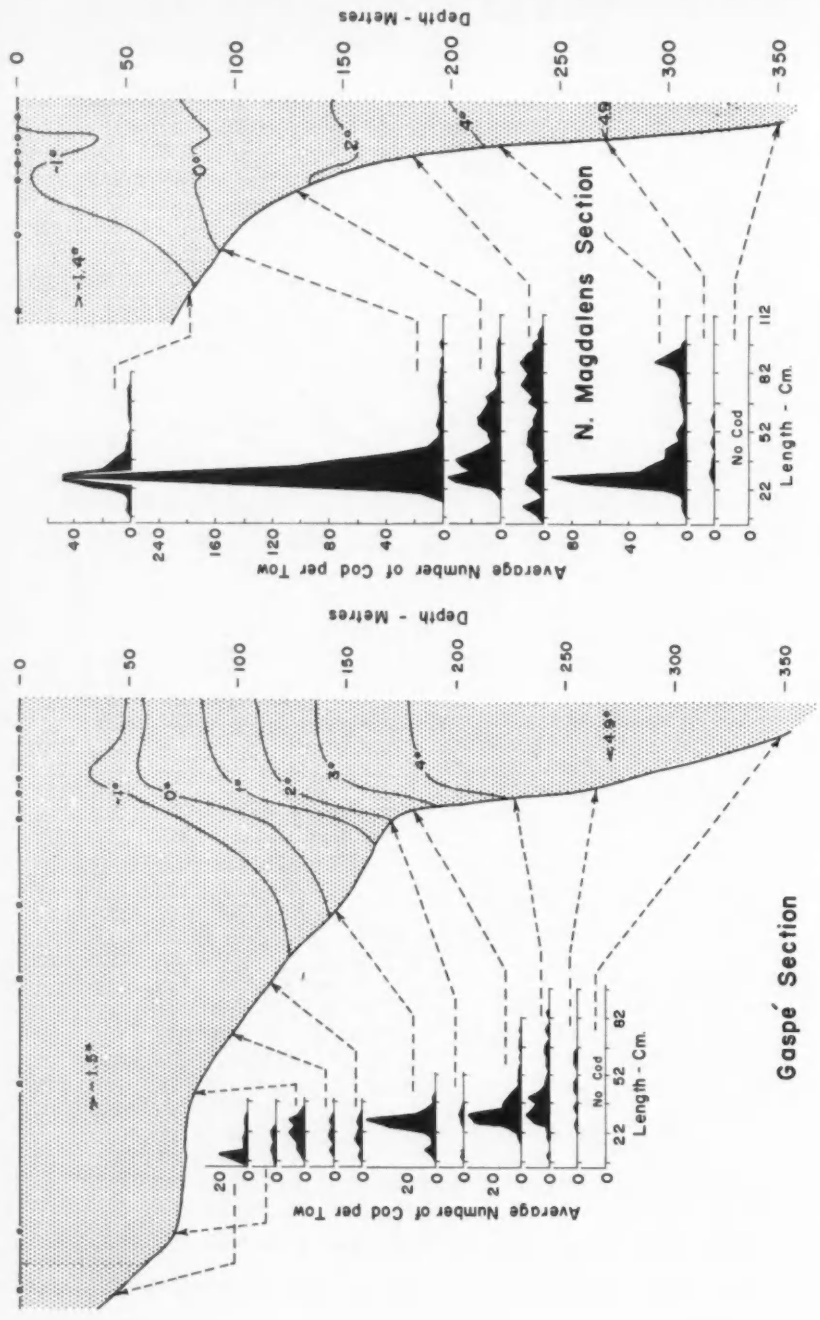


FIG. 3. Distribution of catches of cod by Canadian trawlers in Divisions 4T, 4V and 4W



and 4W (4X omitted) in 1959, from log records. Each dot represents 22.7 metric tons.


Depth - Metres
0
50
100
150
200
250
300
350
-1°
0°
1°
2°
3°
4°
4.9°
≥-1.4°
N. Magdalens Section
Average Number of Cod per Tow
240
160
120
80
40
No Cod
22
52
82
112
Length - Cm.
Depth - Metres
≥-1.5°
-1°
0°
1°
2°
3°
4°
≥4.9°
Gaspé Section
Average Number of Cod per Tow
20
No Cod
22
52
82
Length - Cm.

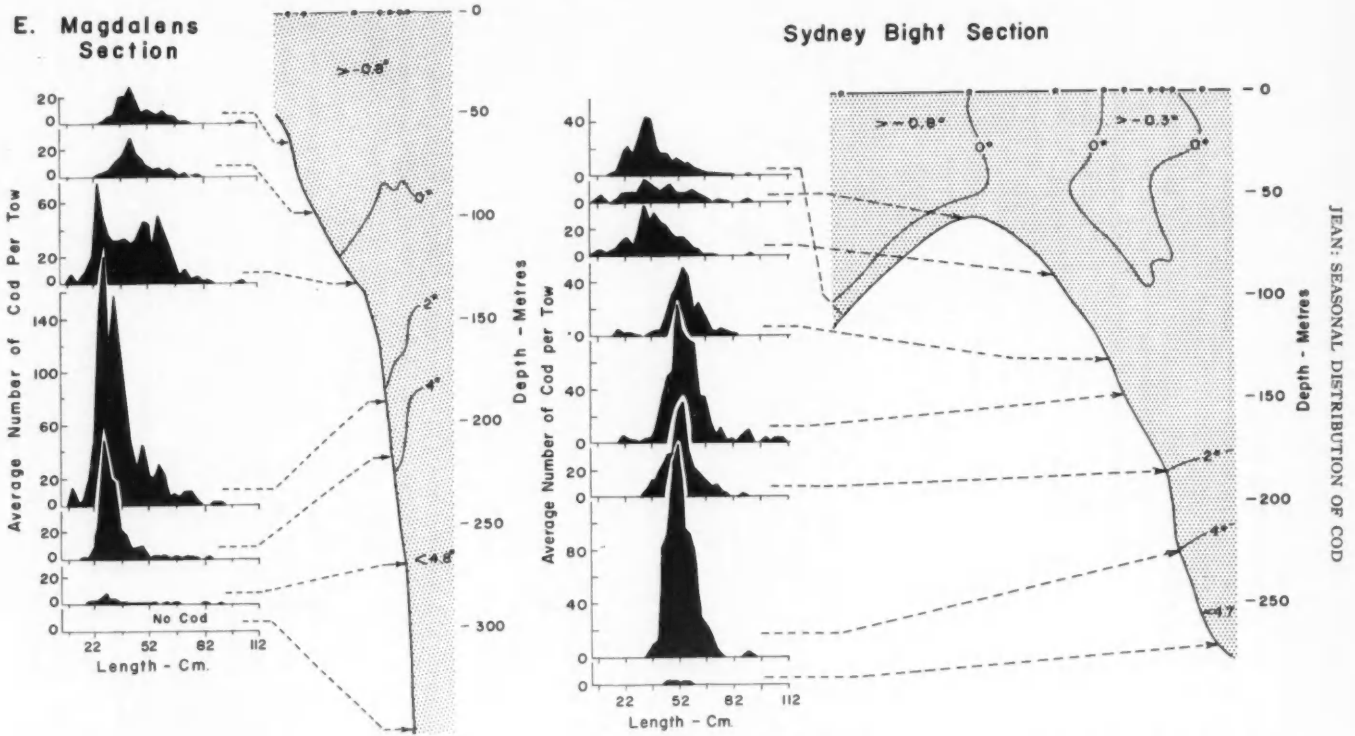


FIG. 4. Size composition of cod in relation to depth and bottom temperature at 4 sections along the southwestern slope of the Laurentian Channel during the winter of 1960.

tities of fish of pre-commercial sizes (22 to about 38 cm) were caught at depths of 150–250 m, and at bottom temperatures of about 2 to 4°C. Very few medium- and large-size cod (39 cm and above) were caught, and they were taken only at 220–250 m and at bottom temperatures around 4°C. In summer, fish of this size are taken in commercial quantities in this area, mainly at depths of about 55–150 m.

The second winter section, north of the Magdalen Islands yielded generally greater catches than off Gaspé. No tows were made at depths of less than 60 m. This may be the reason why cod smaller than 22 cm in length were poorly represented. Catches consisted mainly of cod of pre-commercial sizes (22–38 cm), and these were present from about 80 to 230 m, but mainly at around 100 m. Bottom temperatures where the greatest concentrations occurred ranged from 0 to 2°C. Cod of commercial sizes (39 cm and larger) were taken at depths of 130–230 m and bottom temperatures of 2 to 3°C. Commercial sizes of cod were virtually absent from the Gaspé section.

The third winter section, east of the Magdalen Islands, extending from about 60 to 350 m, yielded pre-commercial-size cod (22–38 cm) in largest quantities at depths of 140–230 m. The bottom temperature at these depths ranged from about 0.5 to 3.5°C. The largest concentrations were at 200 m where bottom temperature was around 2.5°C. They were far more abundant along this eastern section than along that to the north of the Magdalen Islands. Similarly, cod of commercial size (39 cm and larger) were more abundant. They were found at depths of 130–200 m and at bottom temperatures of about 1 to 3°C; but they were rare at depths greater than 250 m and at temperatures above 4°C, as was also the case in the sections farther north.

The fourth winter section in Sydney Bight, off Cape Breton, yielded few cod less than 22 cm but there were fair quantities of pre-commercial-size cod (38 cm and smaller) at depths of 75–110 m and at bottom temperatures of 0 to 2°C. Commercial-size cod (39 cm and larger) were caught in large numbers at depths of about 130–220 m. Greatest concentrations occurred where bottom temperatures were between 1 and 4°C. In contrast to those made farther north, tows made in the Sydney Bight area yielded large numbers of commercial-size cod over a wide depth range. However, cod were virtually absent at depths greater than 250 m, as was the case farther north.

The winter surveys along the western edge of the Laurentian Channel indicate that very small cod (22 cm and smaller, modal size at about 13 cm) were present, although in small numbers, in the shallow waters of the Gulf of St. Lawrence in January 1960. They occurred in the coldest water (about –1.5°C). Presumably these very small fish were the last ones to move into deep water in winter. The fact that they were found at about 150 m in the Magdalen Islands area at that time indicates that they carry out a vertical winter migration but do not move so far as the larger fish. Pre-commercial-size cod (22–38 cm) were found in increasing numbers from north to south, but generally not outside the Gulf of St. Lawrence. They were distributed mainly from depths of about 60 to 200 m. Temperatures at these depths ranged from about 0 to 4°C. Com-

mercial-size cod (39–68 cm) were found east of Magdalen Islands and mostly outside the Gulf of St. Lawrence, in the Sydney Bight area. They were caught at depths ranging from about 125 to 200 m, but mainly at a depth of about 150 m. The temperatures at which commercial-size cod were present ranged from about 1 to 4°C and averaged about 3°C. Large cod (69 cm and larger) were present, although in small numbers, mainly east of Magdalen Islands and in Sydney Bight, at depths greater than 150 m and at temperatures ranging from 2 to 4°C, mainly at 3°C.

Results of winter surveys show that most cod of pre-commercial size (up to 38 cm) do not migrate out of the Gulf in winter. Commercial-size cod (39 cm and larger) appear to be sorted out by sizes as they migrate into deep water and out of the Gulf, the larger fish being found farther south.

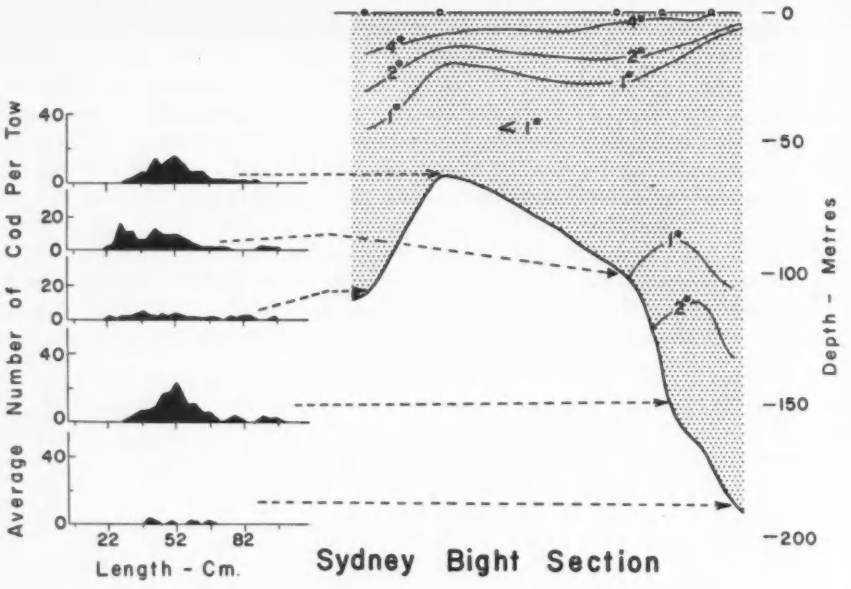
SPRING. The 1960 spring research-vessel surveys (mid May–mid June) were carried out at three of the four sections covered the previous winter: Sydney Bight, east of Magdalen Islands, and Gaspé. The size compositions of cod at various depths for each section are shown in Fig. 5.

Catches of all sizes of cod in Sydney Bight in the spring were small compared to those of the previous winter (Fig. 4). Those cod of commercial size (39 cm and larger) remaining in the region had moved from depths of 130–220 m in winter to 70–150 m in the spring. Bottom temperatures at these depths ranged from about 1° to 3°C. Pre-commercial-size cod which had been most numerous in 75–110 m in winter were almost absent from the spring catches at all depths, suggesting that they leave the area in spring, probably migrating north.

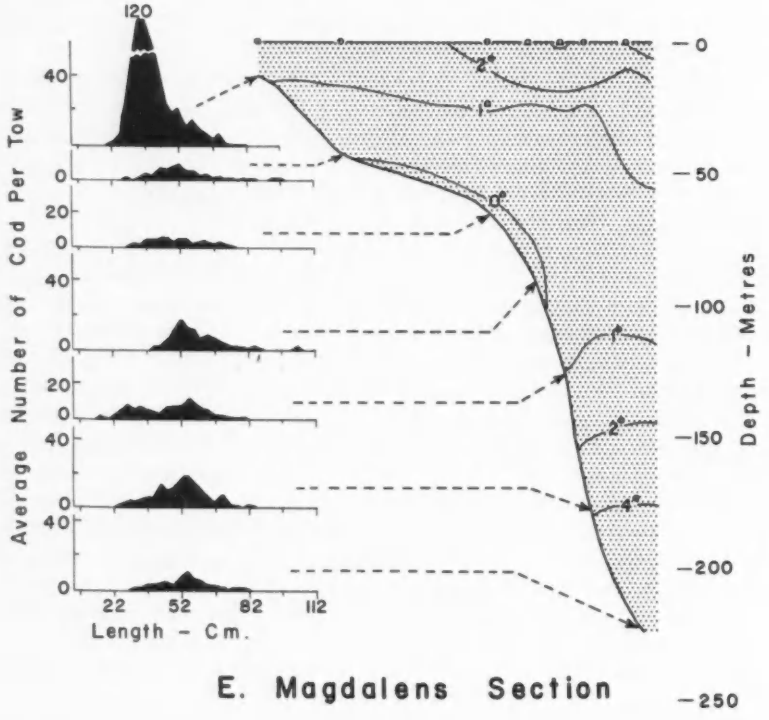
The spring section east of Magdalen Islands included tows from about 25 to 225 m. Large numbers of pre-commercial-size cod (38 cm and below) were taken in shallow water (25 m) and at bottom temperatures of 1° to 2°C. In winter, cod of this size (Fig. 4) were mainly at depths of 140–230 m and at temperatures of 0.5–3.5°C. Pre-commercial-sizes apparently moved into shallow water in spring. Cod of commercial size (39 cm and larger) were found at all depths east of the Magdalens, but were much more abundant both in the shallow water (25 m) above the 0°C isotherm, and in the deep water (deeper than 100 m) than in the intermediate cold-water layer.

To the north, cod had returned in number to the Gaspé section by mid June 1960. Fish of pre-commercial size (38 cm and below) were most abundant at depths less than 55 m in the upper part of the 0°C water layer. Fish of commercial size (39 cm and above) were found at all depths fished down to about 125 m at temperatures from 0° to 3°C, but were most numerous in the upper and lower parts of the 0°C water layer.

Thus, the spring 1960 surveys show that the range of temperatures at which cod of commercial size are found is wider in spring than in winter, namely, from about 0° to about 4°C in spring compared to 1° to 3°C in winter. In spring, they invade the shallow waters along the slopes of the Laurentian Channel where the temperature is still below 0°C. The spring surveys further indicate that cod which are abundant in Sydney Bight in winter leave the area in spring. Likewise, a comparison of winter and spring catches further north along the slope of



Sydney Bight Section



E. Magdalens Section

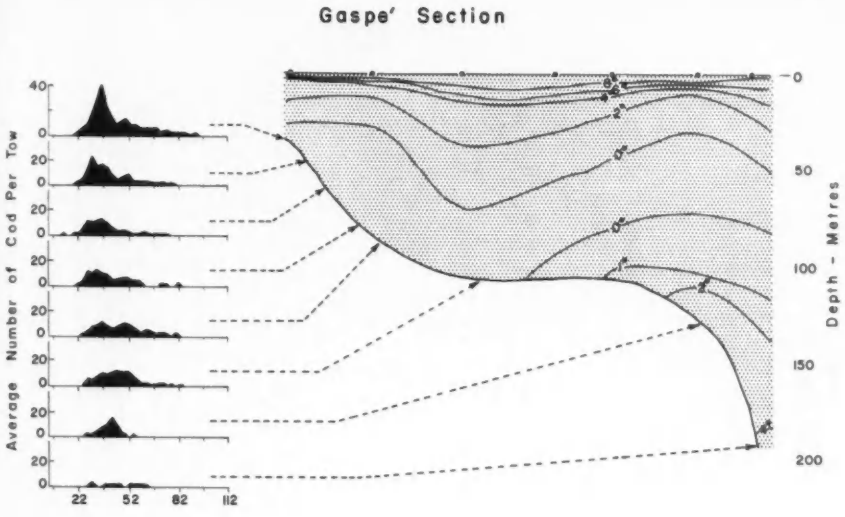
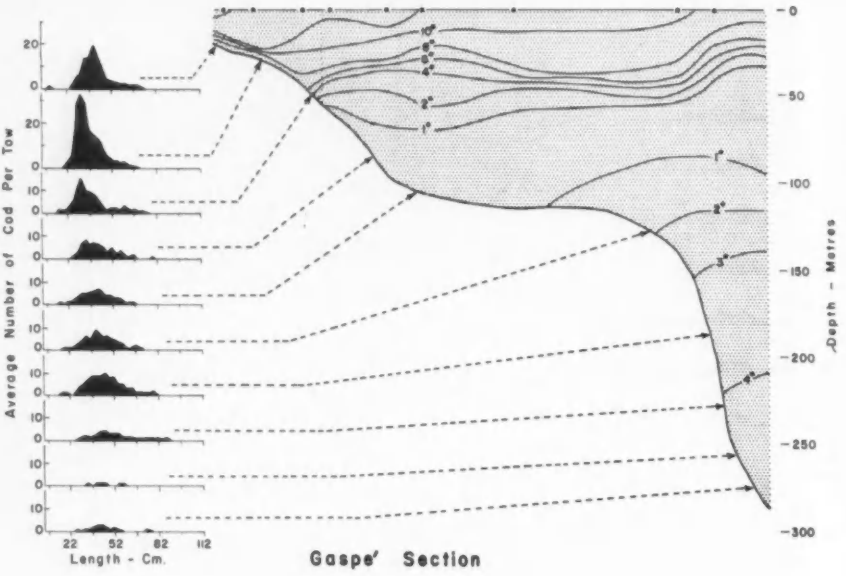
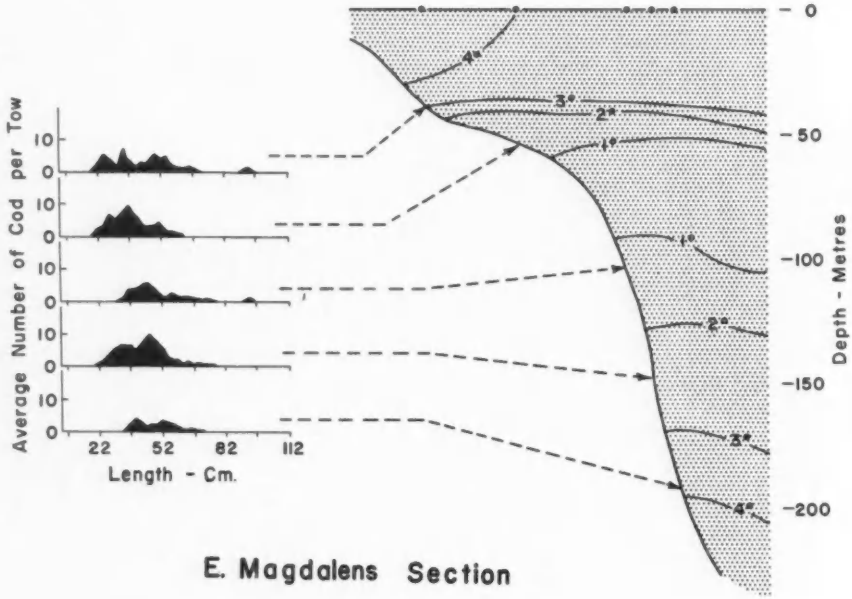


FIG. 5. Size composition of cod in relation to depth and bottom temperature at 3 sections along the southwestern slope of the Laurentian Channel during the spring of 1960.


Average Number of Cod Per Tow
Length - Cm.
22
52
82
112
Depth - Metres
0
-50
-100
-150
-200
-250
-300
Gaspe' Section


Average Number of Cod per Tow
Length - Cm.
22
52
82
112
Depth - Metres
0
-50
-100
-150
-200
E. Magdalens Section

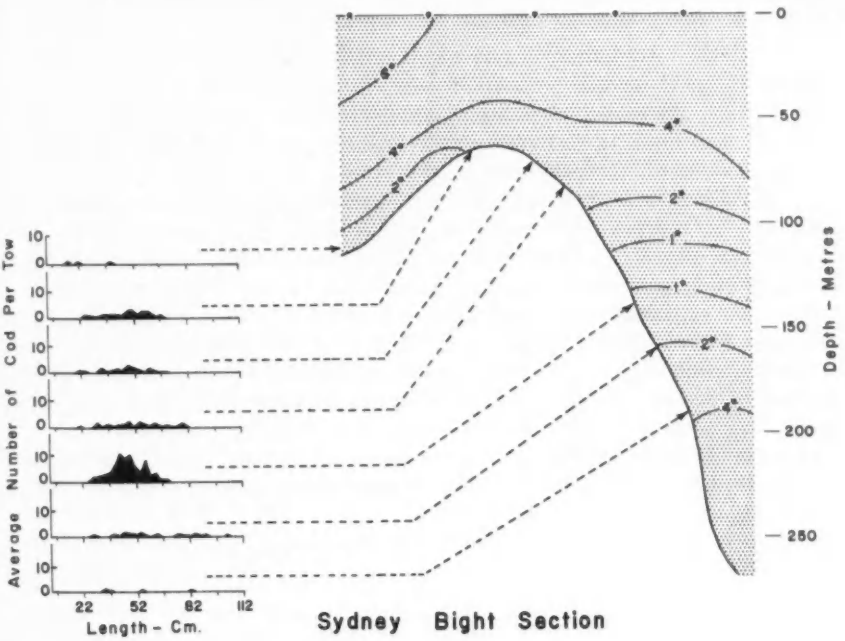


FIG. 6. Size composition of cod in relation to depth and bottom temperature at 3 sections along the southwestern slope of the Laurentian Channel during the autumn of 1960 (except for Sydney Bight section which was covered in the autumn of 1959).

the Laurentian Channel indicates that cod move north in spring from deep to shallow water.

AUTUMN. Autumn 1960 surveys along the western side of the Laurentian Channel (Fig. 6) covered two sections only: Gaspé and east of Magdalen Islands. The Sydney Bight section was not covered in 1960. A survey of this area, however, was made in early November 1959 and the results are included here in Fig. 6, along with the 1960 autumn surveys.

In shallow water off Gaspé (50 m and less) the autumn survey showed large concentrations of pre-commercial-size cod. Bottom temperatures at this depth ranged from 4° to 8°C. These small cod were most numerous at depths just above the cold-water layer and below the thermocline. They were observed feeding heavily on euphausids and small benthic animals (annelids, amphipods, etc.). The thermocline, with temperatures up to 10°C at this period, possibly acted as a barrier to movements into shoaler water, and concentrated these cod close to bottom at a depth of about 50 m. Commercial-size cod (39 cm and above) were also caught in shoal water.

At intermediate depths (60–120 m), cod of all sizes were caught in autumn, but in smaller numbers than in shoal water. Temperatures here were below 1°C. Apparently the cod avoided them.

In deep water (120–180 m), at bottom temperatures between 2° and 4°C, catches increased and included a larger proportion of commercial-size cod (39 cm and above).

Finally, at the greatest depths (over 200 m) and at bottom temperatures higher than 4°C off Gaspé, catches were almost nil.

Along the section east of the Magdalen Islands cod were generally less abundant than off Gaspé in autumn. No hauls were made in water shoaler than 40 m in 1960 but two were made at 27 m in October 1962 (Jean, unpublished data). These caught large quantities of pre-commercial-size cod (38 cm and smaller), indicating that small cod in autumn concentrate in the shallows around Magdalen Islands as well as off Gaspé.

Tows made east of Magdalen Islands in autumn 1960 at 40–200 m showed that, as was the case off Gaspé, commercial-size cod (39 cm and over) were present in small numbers at intermediate depths where the temperature was 1°C but abundant both above and below the cold-water layer, where bottom temperatures were higher than 1°C and lower than 4°C.

Fishing in Sydney Bight in November 1959 produced only very small catches of cod at all depths from 60 to about 180 m. Best catches of cod over 39 cm were made at depths of 140 m and at bottom temperatures between 1° and 2°C. The small catches of cod indicate that they had not moved to these grounds from the Gulf by November 1959.

In conclusion, research surveys of the western edge of the Laurentian Channel showed that, in winter, cod were concentrated at depths of 130–180 m at bottom temperatures of 1° to 3°C. In spring they invaded the shallow waters around the Magdalen Islands and off Gaspé at temperatures of about 0°C but were not abundant in deep water at temperatures higher than 4°C. In autumn

the commercial sizes were caught both above and below the cold-water layer and at temperatures of 1° to about 8°C. Pre-commercial sizes concentrated just below the thermocline in about 50 m.

These results show that, in the Gulf of St. Lawrence, cod are found in a narrower range of temperatures in winter (1–3°C) than in spring (0–4°C) or in autumn (1–8°C).

The 1960 surveys support the conclusions of tagging in the Gulf, which show a migration into deep water and southward in late fall and a return to the Gulf in the spring. Larger cod appear to move farther out of the Gulf than pre-commercial-size cod.

Offshore Nova Scotia Banks Surveys

Research-vessel surveys carried out since 1958 on the offshore Nova Scotia Banks (McCracken, 1964) provided data on the seasonal distribution of cod in relation to depth and water temperature on these banks. Two series of 1960 cruises in late winter (March) and summer (July) were near enough in timing to those carried out in the Gulf of St. Lawrence to permit comparisons. The area covered extended from the southwestern edge of Banquereau southwest to Emerald Bank (Fig. 1) and the data are represented in Fig. 7 and 8.

Winter. A comparison of the winter catches on Banquereau and Emerald Bank (Fig. 7) with those in Sydney Bight (Fig. 4) shows two points: first, Banquereau and Emerald Banks cod were larger, although less abundant, than Sydney Bight cod. Second, winter distribution of cod on Banquereau (Fig. 7) showed maximum concentrations at depths of about 100 m and at temperatures of 3° to 4°C. Few cod were caught around Banquereau at depths greater than 120 m and at bottom temperatures higher than 4°C. In contrast, in Sydney Bight, cod were mainly concentrated at depths of 130–200 m and at bottom temperatures from about 1° to 3°C. In other words, the offshore banks cod in winter were present in shallower, warmer water than Gulf cod.

Winter catches were almost nil at 40 m on top of Banquereau (Fig. 7) where bottom temperatures were lower than 1°C. A series of fishing stations on top of Banquereau in February 1959, at bottom temperatures close to 0°C (Jean, unpublished data), also failed to catch cod. Cod are absent from the top of the banks in winter, presumably on account of cold water that has invaded the surface of the banks.

Winter hauls in the Emerald Bank area (Fig. 7) produced small catches of cod at depths of 110–140 m and at bottom temperatures of 4° to 5°C. These occurred mainly on the western or landward slope of Emerald Bank (Fig. 7, Emerald Bank stations D–G). On the seaward side (Fig. 7, Emerald Bank stations H–M), where bottom temperatures were above 6°C at depths greater than about 75 m, catches of cod were almost nil.

Thus, in winter, offshore Nova Scotia Banks cod were found in shoaler water and at higher temperatures than the cod in Sydney Bight and east Magdalen Islands areas.

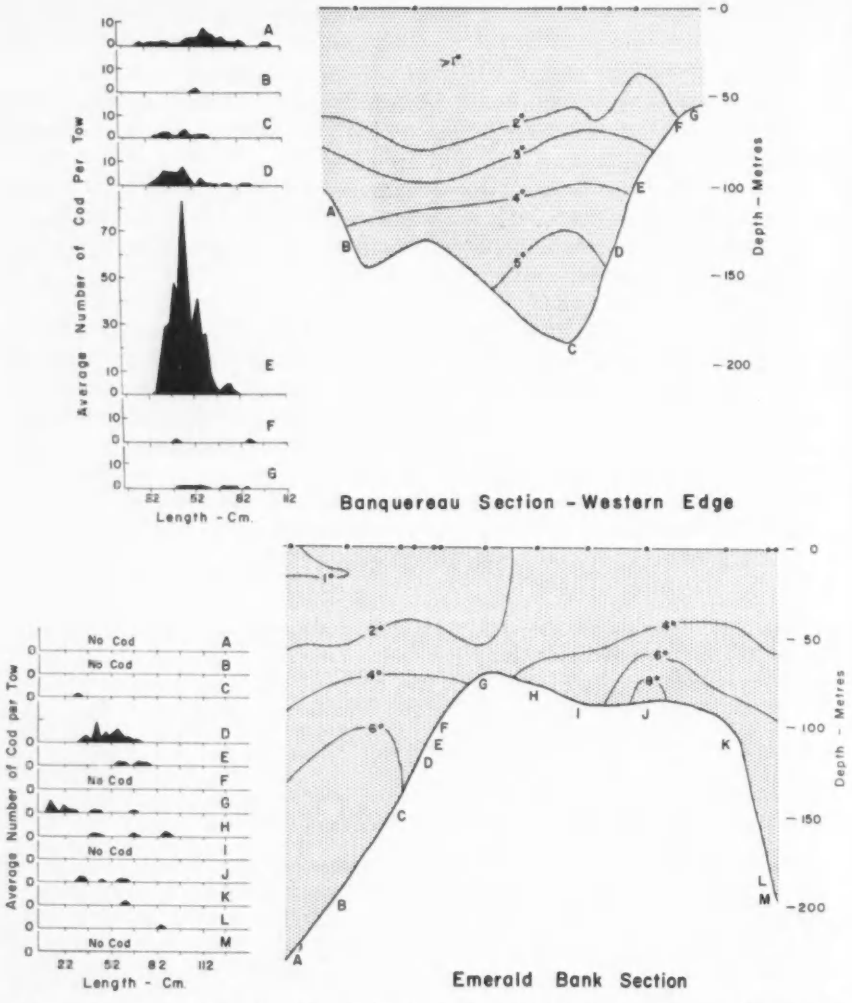


FIG. 7. Size composition of cod in relation to depth and bottom temperature on the offshore Nova Scotia Banks during the winter of 1960.

SUMMER. Research-vessel surveys on the offshore Nova Scotia Banks in July 1960 (Fig. 8) included hauls at depths of 50–100 m on the western edge of Banquereau. Hauls in the Emerald Bank area were made at depths of 70–175 m.

Catches of cod were light in the Banquereau area, but the fish were present in limited numbers at depths of around 50 m (Fig. 8) and bottom temperatures between 4° and 6°C. They were absent at these depths in winter (Fig. 7) when bottom temperature was below 1°C.

Around Emerald Bank summer catches were almost nil (Fig. 8) and came mostly from the top of the bank and shelf area at depths of 80–110 m and temperatures of 4° to 10°C.

Concentrations of cod were not found in research-vessel surveys on offshore Nova Scotia Banks in summer. However, observations showed that offshore banks cod had moved into shallow water and were most numerous at depths of about 50 m and bottom temperatures between 1° and 10°C.

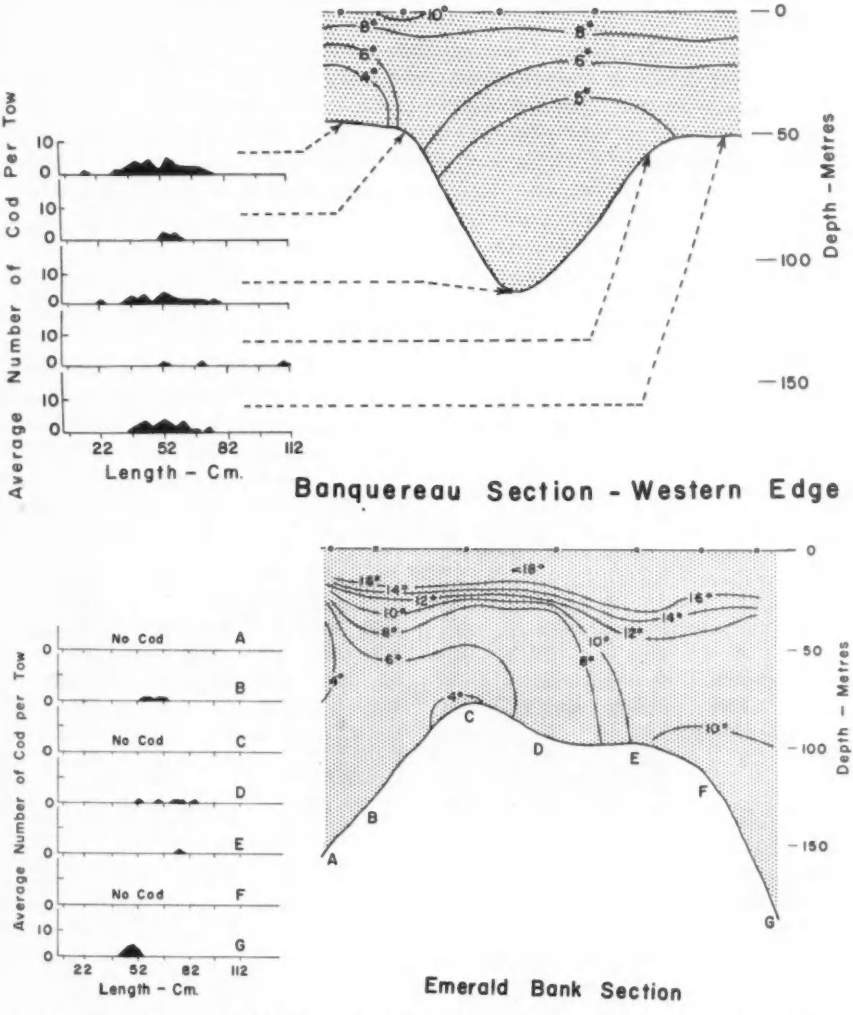


FIG. 8. Size composition of cod in relation to depth and bottom temperature on the offshore Nova Scotia Banks during the summer of 1960.

In conclusion, the seasonal vertical distribution of cod from the Gulf of St. Lawrence south to Emerald Bank shows the following pattern: cod from the Gulf of St. Lawrence and the western edge of the Laurentian Channel are found at greater depths than those from the offshore Nova Scotia Banks, both in summer and winter. In summer cod are taken at depths of 35–145 m in the Gulf of St. Lawrence. On the Nova Scotia Banks they are found, although less concentrated, at about 50 m. In winter commercial-size cod move down to about 130–200 m. Nova Scotia Banks cod of these sizes are found at depths of 90 to about 135 m.

Both Gulf of St. Lawrence and offshore Nova Scotia Banks cod of commercial sizes are found in narrower ranges of bottom temperature in winter than in summer and autumn. In the Gulf the range is about 2C° (from 1–3°C) in winter. In autumn the temperature range increases to about 8C° (from 0–8°C). On the Nova Scotia Banks cod are caught within a temperature range of 2C° (from 3–5°C) in winter. In summer the range increases to about 9C° (from 1–10°C).

Tag returns

The seasonal changes in vertical distribution of cod in Subarea 4 are reflected in the depth pattern of the commercial fishery, as shown by recaptures of tagged cod.

Gulf of St. Lawrence. A total of 5846 cod was tagged and released off northern New Brunswick at depths of 18–110 m during the summer months of 1955 and 1956 (McCracken, 1959). These were cod from the Gulf of St. Lawrence stock. The returns for which depths of recapture were reported to the

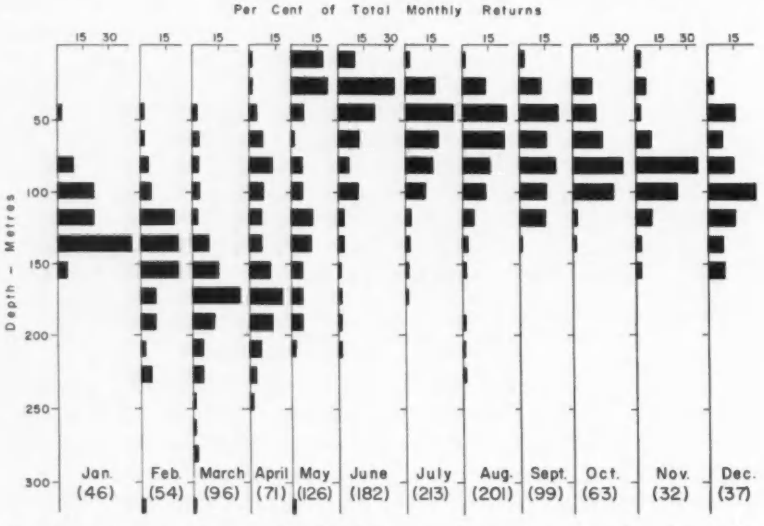


Fig. 9. Returns by month and by depth, of tags released off northern New Brunswick in the summers of 1955 and 1956 (data from McCracken, 1959).

end of 1961 have been grouped by month and by depth. The results are shown in Fig. 9. During January to March, returns came mainly from depths of 130–180 m. The April returns (Fig. 9) showed that cod were mainly below the cold-water layer, but were beginning to spread into shallow water. In May they were both above and below the cold-water layer, i.e. above 50 and below 150 m. In June and July, returns came mainly from depths above 50 m. Finally, from August on, a gradual movement of tagged cod from shallow to deep water is seen (Fig. 9).

In comparing the results of taggings with those of the surveys summarized in the previous section, sizes of cod must be taken into account. Cod tagged in 1955 and 1956 (McCracken, 1959) were of commercial size, i.e. above 39 cm, whereas those caught in the research-vessel surveys included pre-commercial sizes as well. The movement of pre-commercial cod shown by the surveys in the spring (Fig. 5) and the concentration of these small fish in depths less than 50 m in autumn (Fig. 6) would not be shown by the tag returns (Fig. 9).

The presence of commercial-size cod above and below the cold-water layer in April to June, as shown by tag returns (Fig. 9), supports the conclusions of the spring surveys in the Gulf (Fig. 5). The returns of tagged cod in October (Fig. 9) and catches from research vessels during that month (Fig. 6) both show the migrations of commercial-size cod into deep water in autumn.

NOVA SCOTIA BANKS. The returns from winter taggings on the offshore Nova Scotia Banks (Martin and Jean, 1964) have been grouped by quarter and by depth (Fig. 10). Only returns from offshore banks (Divisions 4Vs and 4W) are included. The returns from these areas are grouped by quarter rather than by month because the number of returns is generally too small to be shown by month. The seasonal depth distribution of tag returns from the offshore banks is essentially similar to that from the Gulf taggings. Tags were recaptured on

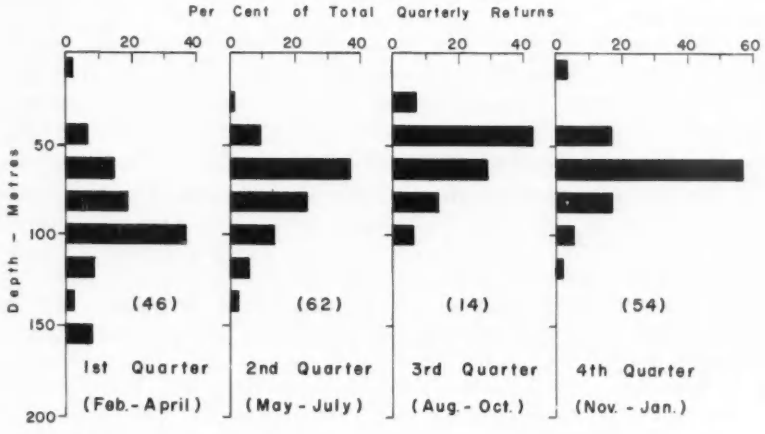


FIG. 10. Returns by quarter and by depth of tags released off Cape Breton and on the Nova Scotia offshore banks in the winters of 1959–62.

the offshore banks in deep water (mainly 100 m) in the first quarter of the year (February–April). During the second quarter they came mainly from 60 to 75 m. During the third quarter (August–October) they were in still shoaler water (40–60 m). Finally, in the fourth quarter, they showed a return movement toward deeper water (60–75 m). A comparison of returns from offshore banks (Fig. 10) with returns from the Gulf (Fig. 9) is consistent with the results of surveys with research vessels. Cod on the offshore Nova Scotia Banks are found in shoaler water than cod from the Gulf of St. Lawrence, at all seasons of the year.

EFFECTS OF SHORT-TERM HYDROGRAPHIC CHANGES ON SURVEY CATCHES

One of the main hydrographic features of the Gulf of St. Lawrence is the presence of a cold-water layer which, except for winter, is found between a warmer surface and a warmer bottom layer (Lauzier *et al.*, 1957; Lauzier and Bailey, 1957). The cold-water layer is defined by Lauzier and Bailey (1957) as the "layer bounded by the 0.0°C isotherms, and thus having temperatures less than 0.0°C". In summer off Gaspé this cold-water layer extends from a depth of about 45 to about 125 m. Most of the fishing grounds of the southwestern Gulf of St. Lawrence, located at depths of 40–140 m, are covered by this cold-water layer. As a result, the summer fishery is carried out in water close to 0°C.

Lauzier and Bailey (1957) have shown that the upper and lower boundaries of the intermediate cold-water layer vary in depth from year to year.

In order to measure the effects of annual variations in hydrographic factors on catches of cod in the Gulf, research-vessel survey catches and hydrographic records collected every summer since 1957 were analyzed. This analysis was limited to the period May to November for two reasons: First, a longer series of observations is available for summer than for winter, and second, the commercial fishery in the Gulf of St. Lawrence, at least for the Canadian fleet, is essentially a summer fishery.

Lauzier and Bailey (1957) used the 0°C isotherms as upper and lower boundaries of the intermediate cold-water layer. In the southwestern Gulf of St. Lawrence, the 0°C isotherms may disappear in summer in some years. For this reason, the 1°C rather than the 0°C isotherms were chosen as the upper and lower boundaries of the intermediate cold-water layer.

From the bathythermograms collected in the southwest Gulf of St. Lawrence during the years 1957 to 1962 the following temperature data were calculated: average depth of upper and lower 1°C isotherms, and the average thickness of the cold-water layer. The thermocline, following Hutchinson (1957), was defined as "the plane of maximum rate of decrease in temperature". This plane passes through the point of inflexion of the BT curve. The average depth of the thermocline was calculated from the BT tracings. A continuous series of observations from 1957 to 1962 was available for two periods, early June and October. BT casts were taken as a rule at approximately the same dates and were therefore comparable from year to year. A summary of hydrographic data and survey catches for the years 1957 to 1962 is given in Table II. The effects of only two

hydrographic features listed in Table II (depths of lower 1°C isotherm and of thermocline) are discussed here. The conclusions which apply to depth of lower 1°C isotherm also apply to thickness of the cold-water layer. Similarly, the depths of the upper 1°C isotherm and the thermocline vary more or less in unison. The effects of depth of thermocline as discussed below apply therefore to depth of upper 1°C isotherm.

TABLE II. Summary of hydrographic data and survey catches of cod in the southwestern Gulf of St. Lawrence during the years 1957–62.

	Hydrography				Catch			
						Av. no. cod per tow		
Year	Av. depth thermocline	Av. depth upper 1°C	Av. depth lower 1°C	Av. thickness cold-water layer	No. of tows	Small[a]	Large[b]	All sizes
	m	*m*	*m*	*m*				
1957								
June	23.2	49.4	130.0	80.6	69	43.7	88.1	131.9
October	43.5	73.2	106.0	32.8	105	127.5	123.7	241.7
1958								
June	17.4	31.0	106.0	75.0	63	6.2	37.2	43.4
October	42.1	60.4	64.0	4.0	55	37.6	109.7	147.3
1959								
June	35.6	45.7	91.5	45.8	28	28.9	48.4	77.3
October	35.6	77.0	104.0	27.0	53	77.6	86.3	164.0
1960								
June	15.6	25.6	110.0	84.4	26	52.7	59.7	112.5
October	40.3	58.5	88.0	29.5	35	85.5	77.4	162.9
1961								
June	27.5	36.6	100.0	63.4	10	37.3	97.1	134.4
October	25.6	38.5	93.0	54.5	34	92.8	99.0	191.9
1962								
June	22.0	40.3	132.0	91.7	26	13.7	80.9	94.6
October	40.3	58.5	128.0	69.5	31	62.2	105.1	167.4

[a]38 cm and below.
[b]39 cm and above.

DEPTH OF LOWER 1°C ISOTHERM

The average number of cod per tow has been plotted against the mean depth of lower 1°C isotherm in Fig. 11. During the years 1957 to 1962 the average depth of the lower 1°C isotherm varied from 64 to 132 m (Table II). As seen in Fig. 11, the points representing average catch, when plotted against depth of lower 1°C isotherm, do not reveal any trend. It would appear that during these months (June and October) the lower 1°C isotherm does not act as a barrier to concentrate cod on bottom.

DEPTH OF THERMOCLINE

The average depth of the thermocline in the southwestern Gulf of St. Lawrence (Table II) varied from about 16 m (June 1960) to about 44 m (October

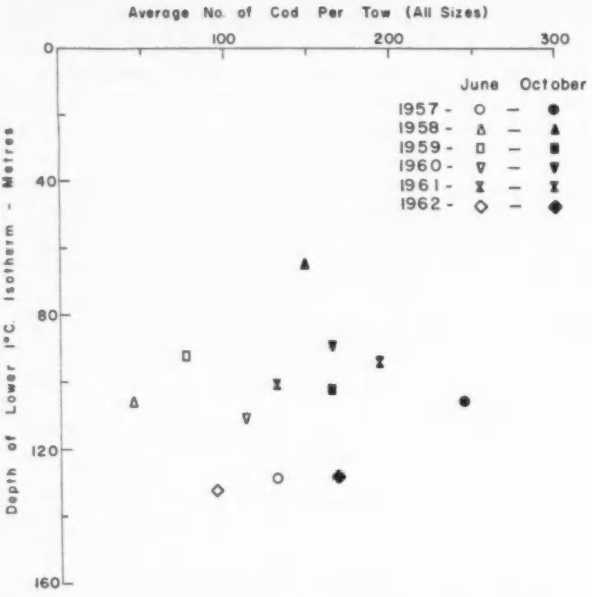


FIG. 11. Catches of cod in relation to depth of lower 1°C isotherm in the southwestern Gulf of St. Lawrence (Division 4T); 1957–62 research-vessel surveys.

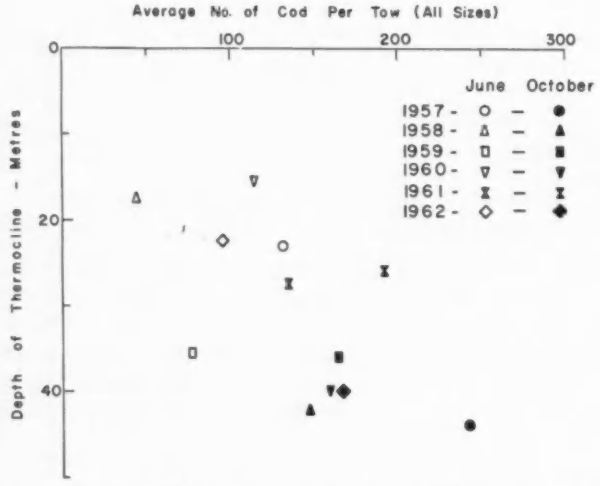


FIG. 12. Catches of cod in relation to depth of thermocline in the southwestern Gulf of St. Lawrence (Division 4T); 1957–62 research-vessel surveys.

1957). The average catch per tow during the June and October cruises from 1957 to 1962 is plotted against mean depth of thermocline in Fig. 12. The relationship between these two parameters is not a very close one. There is, however, a trend (Fig. 12) which would suggest that the lower the thermocline, the larger the catch.

It is possible, however, that larger catches in October than in June (Fig. 12) are due more to greater abundance of cod (through immigration) than to greater availability through concentration by a lower thermocline.

In order to sort out the effects of availability of cod and depth of thermocline on survey catches of cod, the returns from northern New Brunswick releases of tagged fish (McCracken, 1959) are summarized by period of recapture in Table III.

TABLE III. Returns from the southwestern Gulf of St. Lawrence of cod tagged and released off northern New Brunswick in 1955 and 1956 (data from McCracken, 1959).

	Number of tags returned	
Year	May–July	August–November
1957	200	220
1958	138	96
1959	48	37
1960	16	12
1961	12	3
1962	5	3
All years	419	371

The number of returns did not differ appreciably in the two periods. In fact, during May to July, returns were consistently higher than those in August to November. This indicates a roughly comparable abundance of cod in the southwestern Gulf in the two periods.

Larger catches of cod in October than in June, therefore, can be reasonably attributed to the lowering of the thermocline in October, apparently acting as a barrier to upward migrations.

Food and reproduction studies in the southwestern Gulf (Powles, 1958; Lacroix and Marcotte, 1961; Jean, unpublished data) have shown that cod are both feeding and spawning in the Gulf during summer months. Powles (1958) stated that the spawning season of cod extends from May to September. A peak in spawning occurs toward the end of June. Lacroix and Marcotte (1961) have shown that cod in this area were feeding heavily at all stages of gonad development, including ripe and running. These observations confirm those made by the author (Jean, unpublished data) during the summers of 1957 to 1962. It is possible that cod in the act of spawning and/or feeding undertake extensive vertical migrations. The thermocline, however, would act as a barrier. As a result, it is possible that a deeper thermocline concentrates cod near bottom at some seasons, or in some years, thus causing larger catches by otter trawl.

DISCUSSION AND CONCLUSIONS

The present observations are in agreement with the results of morphometric and tagging studies in showing that Subarea 4 cod are divided into several more or less discrete units or stocks. Some stocks (Gulf of St. Lawrence, 4T–4Vn; 4S–4R) migrate extensively; others (Nova Scotia Banks and inshore Nova Scotia, 4Vs, 4W) are less migratory.

As a rule, cod are found in shoaler water and in a wider range of depths and temperatures in summer than in winter.

Seasonal migrations of cod like those in Subarea 4 have been described in stocks from other areas. Trout (1957) has shown that the Bear Island cod move north to the Spitzbergen Shelf in the spring and return to the Bear Island grounds in late autumn. In summer these cod are found in shoal waters (about 135 m). In winter they move to depths of about 350 m. According to Lee (1952), the Bear Island cod are found mainly at bottom temperatures of 1.75° to 3°C in winter and between 3° and 5°C in summer. Templeman and Fleming (1956) have shown that smaller cod on the east coast of Newfoundland move from deep to shoal water in spring. To do so, they move through a cold-water layer (temperature below –1°C). In inshore waters at depths of 10–35 m where temperature is about 5°C in June, they are caught in large quantities as summer progresses in traps set alongshore. However, larger cod remain in deeper water below the cold-water layer at depths of 200 m or more and become the object of a profitable longline fishery. As summer progresses and inshore waters warm, the cold-water layer becomes thinner, and small cod move deeper while large cod move shoreward. In late autumn and winter both small and large cod return to deep water (300 m or more). They remain there until about May.

The present study was not designed to elucidate the problem of cod migrations. The results, however, suggest that the search for preferred temperatures may bring about the seasonal migrations of Subarea 4 cod.

In the Gulf of St. Lawrence (4T–4Vn) cod are present in summer at depths of about 35–145 m and at bottom temperatures ranging from about –0.5° to 8°C. They are most abundant at about 100 m where temperature is around 1°C. In winter they are concentrated in 130–180 m where bottom temperatures are from 1° to 3°C, along the western slope of the Laurentian Channel. Commercial-size cod (above 39 cm) migrate in winter in deeper waters and farther south than small cod.

Research-vessel surveys and records of commercial fishing show that cod are generally less abundant on the Nova Scotia Banks than in the Gulf of St. Lawrence. They are found mainly around Banquereau, Middle Ground, and the northern edges of Sable Island Bank (4Vs and 4W). Farther to the westward, cod are replaced by haddock as the dominant species.

Cod on the Nova Scotia Banks are found in shallower and warmer waters than in the Gulf of St. Lawrence, both in summer and winter. In summer they are present on top (65 m) and on the edges of the banks down to a depth of about 110 m at bottom temperatures ranging from about 1° to 10°C. In winter cod are found mostly at depths of 90–135 m and at bottom temperatures of 2° to 4°C.

In the Gulf of St. Lawrence the depth of the lower 1°C isotherm, which varies from year to year, does not seem to affect availability of cod to the otter trawl. However, the depth of the thermocline apparently does have some effect. A deep thermocline seems to concentrate fish closer to bottom, resulting in larger catches.

Area and depth distributions of commercial catches and of tag returns reflect the seasonal pattern of cod migrations off the Canadian mainland.

RÉSUMÉ ANALYTIQUE

L'influence de la température de l'eau sur la répartition de la morue dans le secteur ouest du golfe Saint-Laurent et sur les bancs de la Nouvelle-Écosse fait l'objet de la présente étude.

En été, la morue de la partie ouest du golfe Saint-Laurent se trouve surtout à des profondeurs de 35 à 145 m, et à des températures de −0° à 6°C. Elle est présente en plus grande abondance à des profondeurs de 100 m et à une température d'environ 1°C. En hiver la morue va vers les profondeurs. On la capture alors à des profondeurs de 130 à 180 m et à des températures de 1 à 3°C.

Sur les bancs de la Nouvelle-Écosse la morue est moins abondante que dans le golfe Saint-Laurent. On la trouve surtout dans la région du Banquereau, du Middle Ground, et le long des accores nord du banc de l'Île de Sable. Vers l'ouest, l'aiglefin remplace graduellement la morue comme espèce dominante. En été comme en hiver la morue des bancs de la Nouvelle-Écosse fréquente des eaux de profondeur moindre et de température plus élevée que la morue du golfe Saint-Laurent. En effet, sur les bancs de la Nouvelle-Écosse la morue en été se trouve surtout à des profondeurs de 65 à 110 m et à des températures de 1° à 8°C. En hiver elle fréquente des profondeurs de 95 à 135 m et des eaux de température de 2 à 4°C.

La répartition saisonnière des prises commerciales de morue reflète bien ses migrations tel qu'on les a observées lors de recensements sur navires de recherches ou encore à la suite de marquages.

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Neotype of *Argis lar* Compared with *Argis dentata* (Crustacea, Decapoda)[1]

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ABSTRACT

The type specimens of *Argis lar* were collected in the north Pacific. They are no longer in existence. Specimens identified as *A. lar* by Rathbun, from the type locality and resembling the original specimens of Owen, are used to set up a neotype. This is done because some authors have assumed that specimens of *Argis* collected in the north Atlantic were *A. lar* and not *A. dentata* which they believed was not a valid species. Also the distribution of both species in northern Canadian waters is not yet clearly understood. Outstanding differences between the two species are discussed.

INTRODUCTION

Owen's type specimen of *Argis lar* was a large female, 4 inches in length. It was accompanied by some smaller paratypes. They were collected in the Bering Sea by Captain F. W. Beechey in the *Blossom* during 1833–34 and were deposited in either the Museum of the Royal College of Surgeons or the Museum of the Zoological Society of London. However, the type material was found to have been lost when searched for after the Museum of the Zoological Society had been disbanded. Later thorough searches also failed to locate it (Dr I. Gordon, personal communication).

It has been found necessary to establish a neotype of this species for two reasons.

(a) Its identity has been confused with that of *Argis dentata* Rathbun. Rathbun (1902, 1904) separated both species in material collected from the type locality (north Pacific). It is likely that Rathbun did not see Owen's type of *Argis lar* but its description fitted one of the species, and she named the other *A. dentata*. Danish authors have not accepted *A. dentata* as a valid species (Hansen, 1908; Stephensen, 1935; Heegaard, 1941). Their specimens were collected in Greenland. Rathbun (1904) states that only *A. dentata* of the genus *Argis* was collected in Greenland by the Princeton Expedition. Also, specimens of *Argis lar* from Greenland that I have examined in the Universitets Zoologisk Museum, Copenhagen, and the British Museum of Natural History, London, were all *A. dentata*.

(b) Although Rathbun (1904) believed that *A. lar* was more of an Arctic species than *A. dentata* she found that both species were taken occasionally over most of their range in the north Pacific. However, *A. lar* has not been

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collected in the Canadian Arctic east of the Beaufort Sea nor in the northwest Atlantic (Squires, 1957, 1963). The identity of both species must be made clear to establish the limits of their distribution in the Canadian Arctic.

SYNONYMY AND DESCRIPTION OF *ARGIS LAR*

[The genus *Argis* (Krøyer, 1842) was erected in a review of the older genus *Crangon* s.l. It takes precedence over *Nectocrangon* (Brandt, 1851). Since Krøyer's specimens were from Greenland, the actual genotype was *A. dentata* which he had identified as *Crangon lar* from Owen's description.]

Argis lar (Owen, 1839)
Crangon lar, Owen, 1839
Nectocrangon lar, Brandt, 1851 (probably in part)
" " Stimpson, 1869 (" " ")
" " Ortmann, 1895 (" " ")
" " Rathbun, 1904

[The specimen here designated as the neotype is an adult female, 17 mm in carapace length. It was captured with 20 other specimens by the U.S. Fisheries Commission Steamer *Albatross* at Station 3251, between Bristol Bay and the Pribilof Islands at 25½ fathoms deep in June 1900. The neotype is labelled as *Crangon lar* Owen, 1839, Catalogue No. 26837, and is deposited in the United States National Museum, Washington, D.C.]

Owen's description is abridged as follows:

"exterior smooth and shining; carapace with 2 spines behind the rostrum one on each side at the anterior margin and another some way behind these; rostrum elevated but truncate at the apex; the eyes immediately beneath the rostrum, their peduncles parallel and in line with the body; 2nd joint of the antennules dilated, spiniform externally, its flagella barely exceeding the antennal scales; antennal scales not exceeding the length of the carapace; dactyls of the 4th and 5th pairs of legs compressed and lanceolate; abdominal segments simply ciliate inferiorly, the first five segments carinate, the last with a double carina which is continued along the telson, towards the end of which they become indicated by lateral spines (Owen, 1839)."

Rathbun (1904) adds to this description as follows:

"carapace about two-fifths or one-third as long as the abdomen; the distance between the two median dorsal spines greater than the distance from the anterior spine to the anterior margin and about equal to or less than the distance from the posterior spine to the posterior margin of the carapace; tubercle sometimes behind the rostral spine; a low blunt irregular carina runs from the orbit nearly to the posterior margin; below this a spine on each side; blade of antennal scale exceeds its spine; chela from 3½ to 4 times as long as the width of the palm: the anterior margin forms an angle of about 45° with the side margin; 1st to 5th abdominal segments with a sharp median carina, 6th segment with two sharp carinae, which toward the end become lower and may disappear altogether in front of the posterior margin; pleura of first 4 segments with rounded entire angles, 5th and 6th segments with an acute tooth or small spine at the postero-inferior angles, 6th segment with a superolateral spine on each side of the posterior margin; the telson with two blunt carinae armed with 3 pairs of spinules on the terminal half. The male is different from the female, smaller, eyes considerably larger; anterior margin of the hand more transverse makes the palm look longer; abdominal carinae are higher and thinner, especially on the 3rd segment; the infero-posterior angle of the 4th segment may have a small spine. The abdomen is more elongate, notably the 6th segment."

Rathbun (1904) further states that the chief differences between *A. lar* and *A. dentata* are that the carinae of the 6th abdominal segment in *A. dentata* end posteriorly in a small sharp tooth or spine, and the chela is longer than in *A. lar*. The chela was said to be 5 times as long as the width of the palm (Rathbun, 1904). Later when writing about *A. dentata* from the Atlantic the length of the chela was said to be 3½ to 4 times the width of the palm, and the spine of the antennal scale was said to exceed the blade (Rathbun, 1929).

DISCUSSION

The features of *A. lar* and *A. dentata* delineated by Owen (1839) and Rathbun (1904) are essentially the same in both species. But there is one exception to this. The morphology of the 6th abdominal segment described by Rathbun (1904) gives a clear difference which may be used to separate the species. Also a few other less obvious differences exist. These are enumerated in Table I.

TABLE I. Comparison of some distinctive features of *Argis lar* and *A. dentata*. Specimens of *A. lar* from between Bristol Bay and Pribilof Islands; 25½ fathoms; June 1960; USNM 26837, and from off Kamchatka; 13 fathoms; June 21, 1900; USNM 26868. Specimens of *A. dentata* from James Bay (Hudson Bay), Lat. 52°55′N, Long. 79°58′W, 60 fathoms, *Calanus* station 59–6, June 23, 1959.

Argis lar (39 specimens)	*A. dentata* (40 specimens)
1. Dorsal carinae of the 6th abdominal segment *low and rounded* posteriorly	Dorsal carinae of the 6th abdominal segment *high and pointed* posteriorly (each carina forming a tooth posteriorly)
2. Three pairs of lateral spines on the telson equidistant or almost so	The median pair of lateral spines on the telson nearer to the distal than to the proximal pair (Fig. 2)
3. A smooth heavy ridge across the 6th abdominal segment dorsally joins the proximal ends of the two carinae	The ridge across the 6th abdominal segment dorsally does not join the proximal ends of the carinae, and has a fringe of short setae directed posteriorly
4. Outer ramus of the uropod almost as long as the inner ramus	Outer ramus of the uropod distinctly shorter than the inner ramus (Fig. 3)
5. Telson with setal fringe scanty in most specimens	Setal fringe on telson profuse in most specimens
6. Sixth abdominal segment 50–70% of carapace length	Sixth abdominal segment 42–58% of carapace length (Fig. 4)

Rathbun (1904) observed that in *A. dentata* the dorsal carinae of the 6th abdominal segment each ended posteriorly in a sharp tooth or spine, while in *A. lar* these carinae virtually disappeared at their posterior ends. The posterior end of the segment is rounded off on both sides dorsally and is lower than the anterior end. The drawing of Owen's type specimen of *A. lar* shows that the end of the 6th abdominal segment is rounded although possibly obscured by the hand colouring (Owen, 1839).

Some other differences in morphology of both species are as follows:

(a) The anterior ends of the dorsal carinae of the 6th abdominal segment are coalesced with the rounded ridge which encircles the segment anteriorly in *A. lar*. In *A. dentata* the ends of the carinae are free from this ridge which has a short fringe of setae (Fig. 1).

(b) The 6th abdominal segment is proportionately shorter in *A. lar* than in *A. dentata* (Fig. 4). Most of the specimens measured were females.

(c) The three pairs of lateral spines on the telson are more nearly equidistant from each other in *A. lar* than in *A. dentata* (Fig. 1 and 2).

(d) The inner ramus exceeds the outer ramus of the uropod by a shorter proportionate amount in *A. lar* than in *A. dentata* (Fig. 1 and 3).

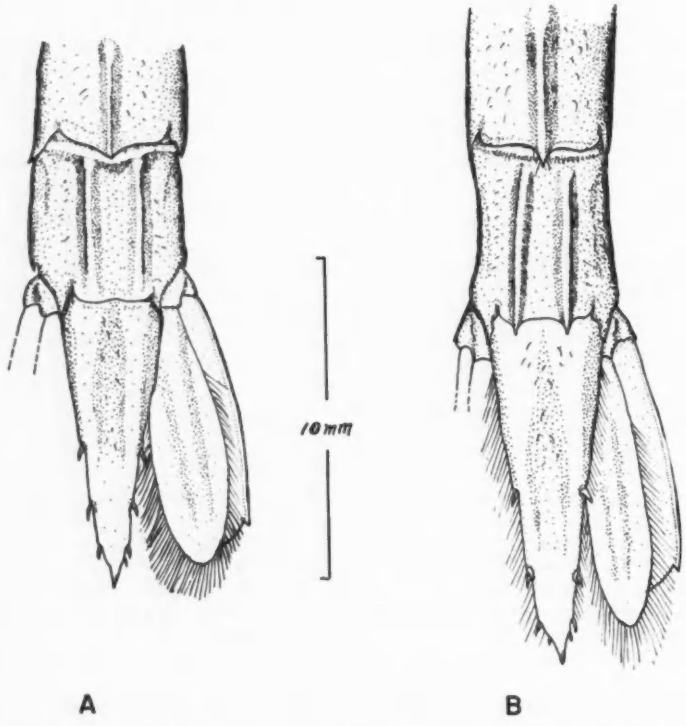

FIG. 1. A: *Argis lar* from between Bristol Bay and the Pribilof Islands, Alaska; 25½ fathoms; June 1900. United States National Museum, 21; Smithsonian Institution No. 26837. (Formerly identified by Mary J. Rathbun.) Drawn from the neotype. B: *Argis dentata* from *Calanus* Expeditions Station 59–6, James Bay, 52°55′N, 79°58′W, 60 fathoms, June 23, 1959. Both specimens were females 17 mm in carapace length.

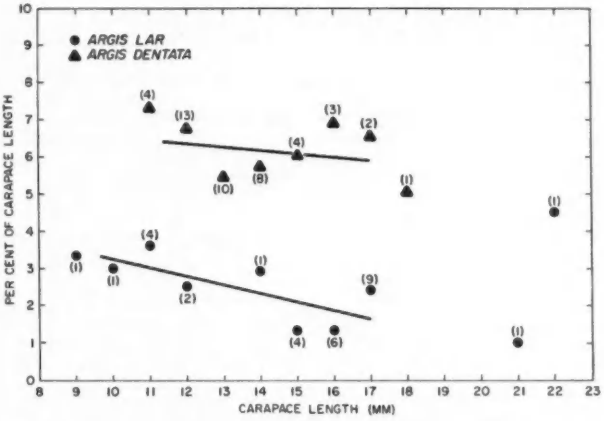

FIG. 2. Average amount by which the distance between the proximal and median pairs of spines exceeds the distance between median and distal pairs (measured between bases of spines), expressed as percentage of carapace length. Numbers in parentheses are numbers of individuals measured at each point.

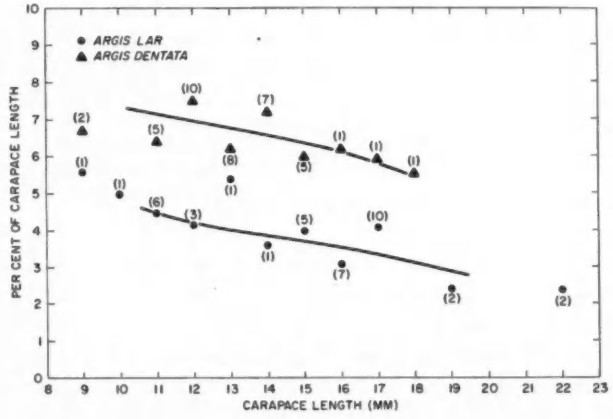

FIG. 3. Average amount by which the length of the inner ramus of the uropod exceeds the outer ramus (measured from the insertion to the tip excluding setae), expressed as a percentage of carapace length. Numbers in parentheses are numbers of individuals measured at each point.

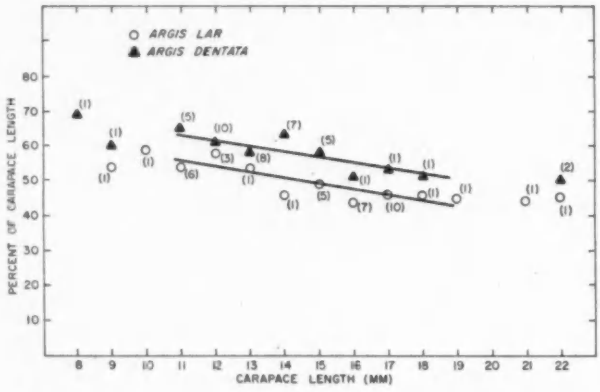

FIG. 4. Average length of 6th abdominal segment (measured from proximal ridge to distal edge, including spines in *dentata*), expressed as a percentage of carapace length. Numbers in parentheses are numbers of individuals measured at each point.

The few specimens of *A. dentata* from the Pacific that I have seen have a considerable number of short setae over the integument generally, giving a somewhat hirsute appearance under magnification. Since Owen (1839) states that his specimens were smooth it is most likely that they were the *A. lar* later recognized by Rathbun (1904) rather than specimens of *A. dentata* which may have been present in the type locality. Also, since specimens of *A. dentata* from the Atlantic are invariably smooth it is possible that there is a difference between the Atlantic and Pacific forms of this species.

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Cod Roe: Component Fatty Acids as Determined by Gas-Liquid Chromatography[1]

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ABSTRACT

The component fatty acids of cod roe resemble the flesh lipid fatty acids to a considerable degree. Comparison with the liver lipids of male and female fish suggests that less essential longer-chain monounsaturated fatty acids from the liver depot fat are metabolized by the female for the synthesis of particular fatty acids required by the developing eggs.

INTRODUCTION

Cod roe (or eggs) are of little direct economic importance in Canadian fisheries, although modest amounts are consumed in various other countries. The significance of the roe lies more in the fact that during the later stages of sexual maturity the fish cease feeding and further development of the eggs is based on withdrawal of body materials. In the formation of the lipids of cod roe it is probable that these are drawn from the liver, whereas in fatty fish the body depot fats are utilized.

The survival of the species (*Gadus morhua*) reflects the fecundity of the female, the eggs released by even a moderate size female numbering in the millions (Powles, 1958). Once spawned the eggs of cod are pelagic, forming an appreciable part of the plankton at the appropriate season (McKenzie, 1940). The fertility of the eggs may be low, but in any event the bulk of the lipids involved is immediately recycled into the food chain through the plankton-eating species.

The present study is intended to explore the fatty acid composition of cod roe and the female liver in relation to other recent observations on cod lipids from a male cod of the same local population.

EXPERIMENTAL

A female cod (*Gadus morhua*) taken in early May at Terence Bay, Nova Scotia (length 83 cm, weight 5.19 kg) was sacrificed within a few hours of being caught. The stomach was empty and the low liver weight (96.8 g, 1.9% of the fish) indicated that the fish had probably not been feeding for some time. The gonads (182.8 g, 3.5% of the fish) were classified as ripening (Powles, 1958) and the weight proportion of gonads also fits the curve for mature female cod from Norwegian waters (Braekkan, 1958).

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The total lipids, extracted by the method of Bligh and Dyer (1959), were 1.4%. The proportion of nonsaponifiable material was 13.6% by the appropriate method of the American Oil Chemists' Society. The recovered fatty acids were esterified with methanol–HCl and the iodine value of these esters was found to be 200 by hydrogenation (*cf.* Notevarp, 1961).

The liver was involved in another experiment and only part was analysed, employing a large volume of petroleum ether for the extraction. Some loss of phospholipid may have resulted from this recovery procedure (Bailey, 1952), but the iodine value (150) for the esters from the recovered fatty acids is normal and compares with 155 for the male fish studied (Ackman and Burgher, 1964).

Gas–liquid chromatography of the methyl esters was carried out on several polyester columns, employing a Barber-Colman Model 10 gas–liquid chromatograph with argon ionization detector. Identification and quantification procedures followed those outlined earlier (Ackman and Burgher, 1964). The iodine values computed from these analyses were 205 for the cod roe esters and 148 for the cod liver. The proportion of branched chain acids in the roe appeared to be less (about 0.1%) than in other cod lipids recently analysed.

The current shorthand notation for fatty acids of "chain length: number of double bonds" is used throughout this paper, and the structures of the unsaturated acids so designated are those detailed in Table II.

REVIEW

Little appears to be known on the composition of cod eggs or roe, although an alkali isomerization study (Notevarp, 1961) for cod roe gives fatty acid proportions by number of double bonds in general agreement with the present results. Before discussion of the latter in detail, it is advantageous to review information on other species, such as the Salmonidae and the Clupeidae.

Salmonidae

The pioneering work of Lovern (1934, 1936, 1942; *cf.* Hilditch, 1956) on the fatty acid composition of maturing eggs of the Atlantic salmon (*Salmo salar*) is not strictly relevant since the changes, as emphasized by this author, include those inherent in the physiology associated with the transition of the adult from salt to fresh water. Thus the initial adult depot fat and egg fat may both be marine in type, but the mature egg contains fatty acids more typical of fresh water species. The fatty acid studies chiefly involved the egg oil (essentially triglycerides), possibly more than half of the total lipid (Smith, 1952, 1957; Kyte, 1956; Bailey, 1952a; Hilditch, 1956a).

According to Smith (1952) the roles of the phospholipids and triglyceride lipids are separate in the development of trout eggs, the former being continuously but slowly metabolized while the latter are not utilized for energy until well after hatching.

Clupeidae

The changes observed in the salmon eggs were not paralleled in less extensive studies by the same author on herring eggs (Lovern, 1936).

The egg lipids of the pilchard or Pacific sardine (*Sardinops caerulea*) in relation to diet, ovarian maturation, and mesenteric fat composition, have been examined with the aid of gas–liquid chromatography (Lasker and Theilacker, 1962). The total lipids were studied, including on a dry weight basis some 11% phospholipid and 4% triglyceride fat (Lasker, 1962). The results may therefore largely reflect the phospholipid composition.

The comparative gas–liquid chromatographic analyses of these authors may be considered satisfactory, but the absolute fatty acid compositions given require correction for comparison with other data. Roughly, the corrections (Edwards and Marion, 1963) would result in a 40% reduction in 16:0 and 18:1, a 30% reduction in 18:0 and 18:1, a slight increase in the 20:5, and a 40% increase in the 22:6. On this basis the results for the 16:0, 16:1, 20:5 and 22:6 are of the same order as the results for cod roe fatty acids (Table I), but there is a substantially lower level for 18:1. In the mesenteric fat the level of the latter acid was higher than in the eggs, very noticeably so in the males. This fish is reported either not to feed actively in the pre-spawning migratory period (Bailey, 1952), or to feed up to the time of spawning (Hand and Berner, 1959). However, Lasker and Theilacker (1962) demonstrated that feeding an artificial diet (trout food) influenced the mesenteric fat to a considerable degree, and to some extent the ovarian fat as well. Thus the diet high in 18:1 and low in the longer-chain polyunsaturated acids resulted in an increased level of 18:1 in both the mesenteric fats and the ovarian fat, whereas the proportions of 20:5 and 22:6 remained low in the mesenteric fat but approached normal levels in the ovarian fat.

The fat of a copepod (*Calanus helgolandicus*) prominent in the natural diet of this species, was also analysed and was similar in composition to the natural ovarian fat, especially in the low level of 18:1. On the other hand, as stated above, the mesenteric fat of fish on this diet was within the normal range for marine depot fats in respect to this acid (*cf.* Klenk and Eberhagen, 1962), although lower in 14:0, slightly lower in 20:5, and appreciably lower in 22:6, in relation to the copepod fat.

It may be concluded that in this species the fish attempts to optimize the ovarian fat to a certain fatty acid composition irrespective of diet and any corresponding changes in depot fat composition. The similarity of the ovarian fat in composition to that of the copepod is superficial, and the conclusions of these authors that the fish has little metabolic control over ovarian fatty acid composition may be challenged on their own evidence. This similarity may be due to coincidence or to environmental advantages conferred on both the copepod and the pelagic sardine egg or larvae (*cf.* Lasker, 1962) by a fatty acid composition of this type.

In the case of the capelin (*Mallotus villosus*) a preliminary study (Ackman *et al.*, 1963) of the total lipids of the mature fish indicated that the roe lipids of the female influenced the iodine values of the oil (female 144, male 125) through a higher proportion of 20:5 and 22:6 coupled with a lower proportion of monounsaturated fatty acids of these chain lengths. Only a slight increase in 18:1 was observed in the female.

TABLE I. Composition in weight per cent of the methyl esters of fatty acids from cod roe.

Complete analysis			Chain length analysis		
				Hydrogenated	
Fatty acid			Unhydrogenated	Argon	Flame
14:0	–	0.6	0.7	0.6	0.6
14:1	?	NSA			
15:0	–	0.1	0.1	0.1	0.1
15:1	?	NSA			
16:0	–	23.4	29.9	30.7	28.7
16:1	9[a]	6.4			
16:2	6, 9	NSA			
16:2	9, 12	0.1			
16:3	6, 9, 12	TRA			
16:4	6, 9, 12, 15	NSA			
17:0	–	NSA	0.1	0.1	0.1
17:1	?	0.1			
18:0	–	1.3	25.1	24.7	23.8
18:1	9[a]	23.4			
18:2	6, 9	NSA			
18:2	9, 12	0.2			
18:3	6, 9, 12	0.1			
18:3	9, 12, 15	0.1			
18:4	6, 9, 12, 15	0.1			
19:0	–	NSA	0.1	0.1	TRA
19:1	?	0.1			
20:0	–	NSA	20.1	20.3	21.4
20:1	11[a]	1.0			
20:2	8, 11	NSA			
20:2	11, 14	TRA			
20:3	...	NSA			
20:4	5, 8, 11, 14	2.4			
20:4	8, 11, 14, 17	0.1			
20:5	5, 8, 11, 14, 17	16.5			
21:0	–	0.0	TRA	TRA	TRA
21:5	?	TRA			
22:0	–	NSA	23.1	23.3	24.6
22:1	11[a]	0.2			
22:4	7, 10, 13, 16	NSA			
22:5	4, 7, 10, 13, 16	0.1			
22:5	7, 10, 13, 16, 19	0.7			
22:6	4, 7, 10, 13, 16, 19	22.1			
24:0	–	NIL	0.8	0.5	0.7
24:1	?	0.8			

[a]Other isomers may be present.
NIL — none present.
NSA (no significant amount) — possibly present, but $<<0.1\%$.
TRA (trace) — present, but $<0.1\%$.

GENYPTERAE

Shorland (1939) has examined the New Zealand ling (*Genypterus blacodes*) and found that the fatty acids of the triglycerides of the roe resembled those of the liver oil, and were lower in the longer-chain polyunsaturated fatty acids than the phosphatides of the roe.

DISCUSSION

Although the complete analysis (Table I) of the fatty acids of cod roe is of interest since no comparable figures have been published, the comparison of certain key fatty acids with other data from cod lipids (Table II) is more informative. The general composition of the cod roe lipids suggests that of the flesh lipids (from a male taken in the same locale at the same time of year) in the low level of 20:1 and 22:1, but differs in having a higher proportion of 16:1 and particularly of 18:1, while the level of 22:6 is not as high. In part, this may be due to a significant triglyceride content in the roe in contrast to the flesh which is largely phospholipid (Bligh, 1961).

TABLE II. Percentages of some significant fatty acids (as methyl esters) in the roe of a female cod, the liver of the same cod, and of the liver and flesh of a male cod taken at the same location at approximately the same time.

Fatty acid	Double bond positions	Female		Male	
		Roe	Liver	Liver[b]	Flesh[c]
16:0	–	23.4	11.5	10.4	24.1
16:1	9[a]	6.4	14.0	12.2	1.1
18:0	–	1.3	2.1	1.2	3.4
18:1	9[a]	23.4	31.5	19.6	7.8
18:2	9, 12	0.2	0.6	0.8	0.3
20:1	11[a]	1.0	5.0	14.6	1.2
20:4	5, 8, 11, 14	2.4	0.9	1.2	3.5
20:5	5, 8, 11, 14, 17	16.5	11.4	5.0	17.6
22:1	11[a]	0.2	3.2	13.3	1.1
22:5	7, 10, 13, 16, 19	0.7	0.9	1.9	0.6
22:6	4, 7, 10, 13, 16, 19	22.1	10.2	10.5	37.5

[a]Other isomers may be present.
[b]Ackman and Burgher (1964).
[c]Ackman and Burgher (1964a).

According to Dambergs (1963) the flesh lipid content of males and females differs only slightly in mature Terence Bay cod taken in the fall period of normal feeding activity. Although it has been suggested (Bogucki and Trzesinski, 1949) that Baltic cod undergo severe seasonal fluctuations in flesh lipid content, the latter being inversely proportional to liver fat level, other evidence suggests that seasonal variations in flesh lipid level are not significant in North Sea cod (Olley and Lovern, 1960). Provisionally it may be considered that the flesh lipid level variations and possibly the flesh lipid fatty acid composition changes are small in cod, when compared to liver fatty acid variations.

When the cod roe composition is compared with the liver of the same fish and with the male liver, marked differences are apparent. Thus the female liver has an increased level of 18:1 and 20:5 when compared to the male liver, and this is reflected in the roe composition. The levels of 20:1 and 22:1 in the female liver are somewhat low for a marine depot fat (*cf.* capelin studies, Ackman *et al.*, 1963; cod liver lipids, Ackman and Burgher, 1964; Klenk and Eberhagen, 1962) and it may be inferred that these acids are being withdrawn for metabolic needs in the non-feeding period. If this was strictly for energy needs the male liver should be comparable, but since the levels of these acids are much higher in the male, the female may be breaking them down for synthesis of 18:1, 20:5 and 22:6 needed by the developing eggs.

In the male cod it was observed that the proportions of the three major polyunsaturated fatty acids (20:4, 20:5 and 22:6) were the same (about 1:5:9) in both the liver and the flesh (Ackman and Burgher, 1964a). In the female the proportions of all three acids are not in the same accord in either the liver or in the roe, but the ratio of 20:4 and 22:6 is the same as previously observed in the male (1:9). The latter two acids are not metabolically related, but the 20:5, which is present in higher proportions in the two female lipids, is a precursor of the 22:6 (Mead, 1961). It is probable that the higher level of 20.5 in the female liver represents both an accumulation for direct deposition in the roe as necessary, and also a pool for synthesis of the 22:6. Further studies on this same population are in progress and may be expected to provide further information on these fatty acid relationships.

CONCLUSIONS

Assessment of earlier work on salmon and Pacific sardines, combined with the present results, indicates that the fatty acid composition of fish egg lipids is probably distinctive for each species and not necessarily related to the diet or depot fat of the adult. The adult fish, when feeding, may derive certain fatty acids necessary for the development of the roe lipids from the diet, or may synthesize them, but when not feeding in the pre-spawning stage it breaks down less essential fatty acids from the depot fat to form those fatty acids necessary for the appropriate fatty acid composition of the egg.

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Some Alternative Premises for Constructing Theoretical Reproduction Curves[1]

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ABSTRACT

Various types of reproduction curves have found extensive use in management and analysis of fish populations. To these may be added curves based on depensatory processes of mortality. Life-history stages may be considered as successive "stock and recruitment" relationships, the output from one process comprising the input of the next. A variety of reproduction curves can thus be generated by considering differing sequences of compensatory and/or depensatory processes.

Reproduction curves have been extensively used in management and analysis of fish populations since their development by Ricker (1954). Some types of curves which have been reported are shown in Fig. 1–4 and include:

(1) Compensation curves of the family

$$Z = we^{a(1-w)} \tag{1}$$

which describe a compensatory population regulation, progressively more severe in compensation with increase in stock size (Ricker, 1954).

(2) Quotient curves of the type

$$Z = \frac{w}{1 + A(w-1)} \tag{2}$$

suggested by Beverton and Holt (1957), which describe an asymptotic compensation mechanism.

(3) Empirical curves, based either on reasonable premise (e.g. Ricker, 1958a, curves F and G; and Ricker, 1958b, for various kinds of situations), or based on curves fitted to observation (e.g. Shepard and Withler, 1958).

(4) Modified compensation curves of the form

$$Z = we^{\text{absgn }(1-w)a|1-w|^b} \tag{3}$$

in which the modifying exponent b is added to the term $(1-w)$ treated as positive, but preserving the sign of $(1-w)$ as an exponent of e. Curves of this family (Fig. 3 and 4) introduce sinuosities into the stock–recruit relation which may be useful in simulating some natural situations, for example, when territorial behavior prevents supersaturation of spawning areas (Di Costanzo, personal communication).

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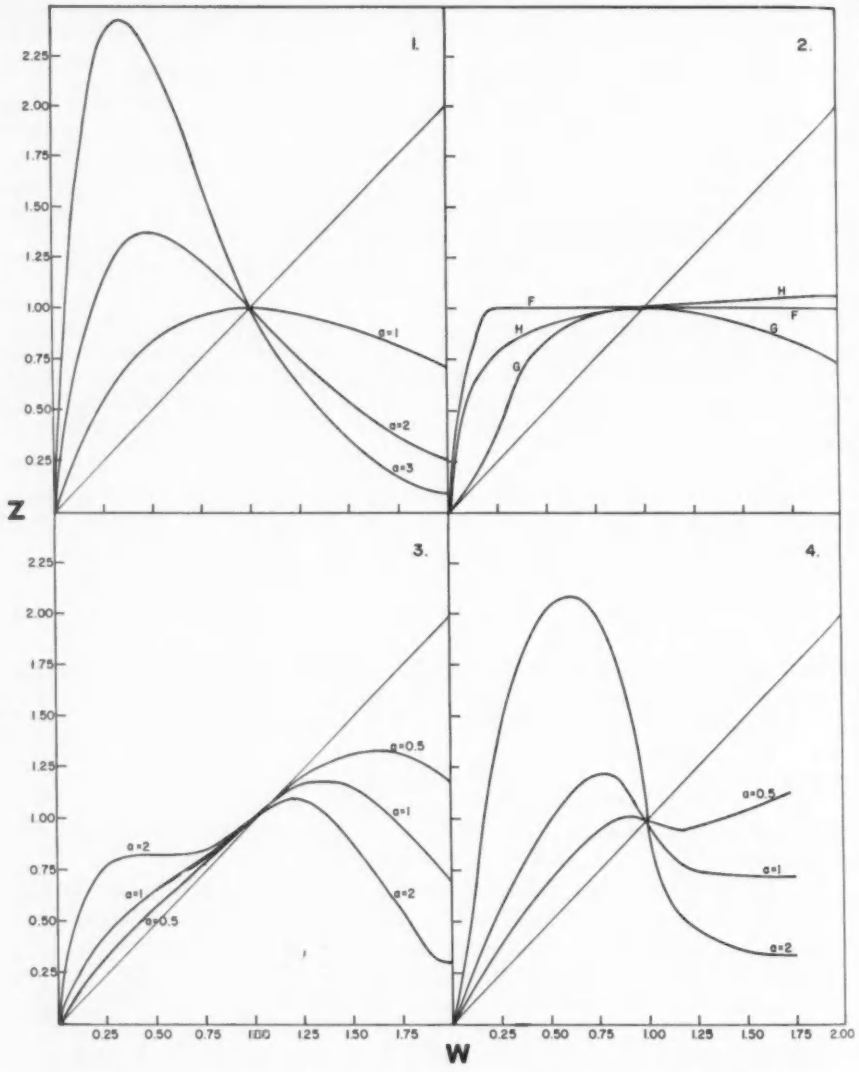

FIG. 1. Reproduction curves based on the compensation formula $Z = we^{a(1-w)}$

FIG. 2. Various reproduction curves after Ricker (1958a, b).

(F) $Z = we^{a(1-w)}$, $a = 2$ up to 1.0

(G) $Z = we^{a(1-w)}$, $a = 1$ beyond $w = 0.4$

(H) $Z = \frac{w}{1 + A(w-1)}$, $A = 0.9$

FIG. 3. Modified compensation curves with the formula $Z = we^{a(1-w)^b}$ where $b = 2$.

FIG. 4. Modified compensation curves with the formula $Z = we^{a(1-w)^b}$ where $b = 0.5$.

This paper outlines some alternative premises for constructing theoretical reproduction curves, and deals largely with the consequences of considering life history stages as successive "stock and recruitment" relationships.

DEPENSATION CURVES

Ricker (1954) presented a classification of predation into three types:

"A" in which a fixed number of prey are taken,

"B" in which predators at any given abundance take a fixed proportion of prey, and

"C" in which predators take all of the prey in excess of a certain number.

The familiar compensation curve represented by equation (1) results from a formulation of cannibalism, but may also be related to Type B predation if there is a numerical response by the predator.

The consequences to a stock–recruitment relation of Type A predation and Type B predation with a fixed number of predators, *if they were the only factors operating*, are shown in Fig. 5. Type A predation expressed as a consequence in a stock–recruitment relation has the form

$$Z = we^{a} - C \tag{4}$$

where C is the fixed number of prey taken by the predator. As indicated in Fig. 5, the population will increase or decrease indefinitely depending on whether we^{a} is greater or less than C. The proportion taken by the predator is smallest for the largest populations, the ratio of Z to W increasing with increase in W.

Type B predation for a given abundance of predators expressed in terms of its consequences to the stock–recruitment relation has the form

$$Z = we^{a-b} \tag{5}$$

where b represents the fixed instantaneous rate of mortality caused by the predator. Curve F of Fig. 5 where $C = 0$ is an example. The ratio of Z to w is a constant, and provided $a > b$ the population increases indefinitely.

Types A and B may be combined into the more general form

$$Z = we^{a-b} - C \tag{6}$$

which may be called a linear depensation curve wherever C is greater than zero.

An alternative depensation curve is provided by

$$Z = we^{aw} - C \tag{7}$$

a process which relates the intensity of depensation logarithmically to density.

An obvious feature of the above depensation curves is the implication that at certain stock densities all of the prey will be "captured". It would seem more reasonable to suppose that at even the lowest densities of stock some prey would survive. In more general terms, for any depensatory process, it might be expected that there would not be a sharp threshold below which all prey are taken, but rather there would be a continuous and decreasing effect at increasing

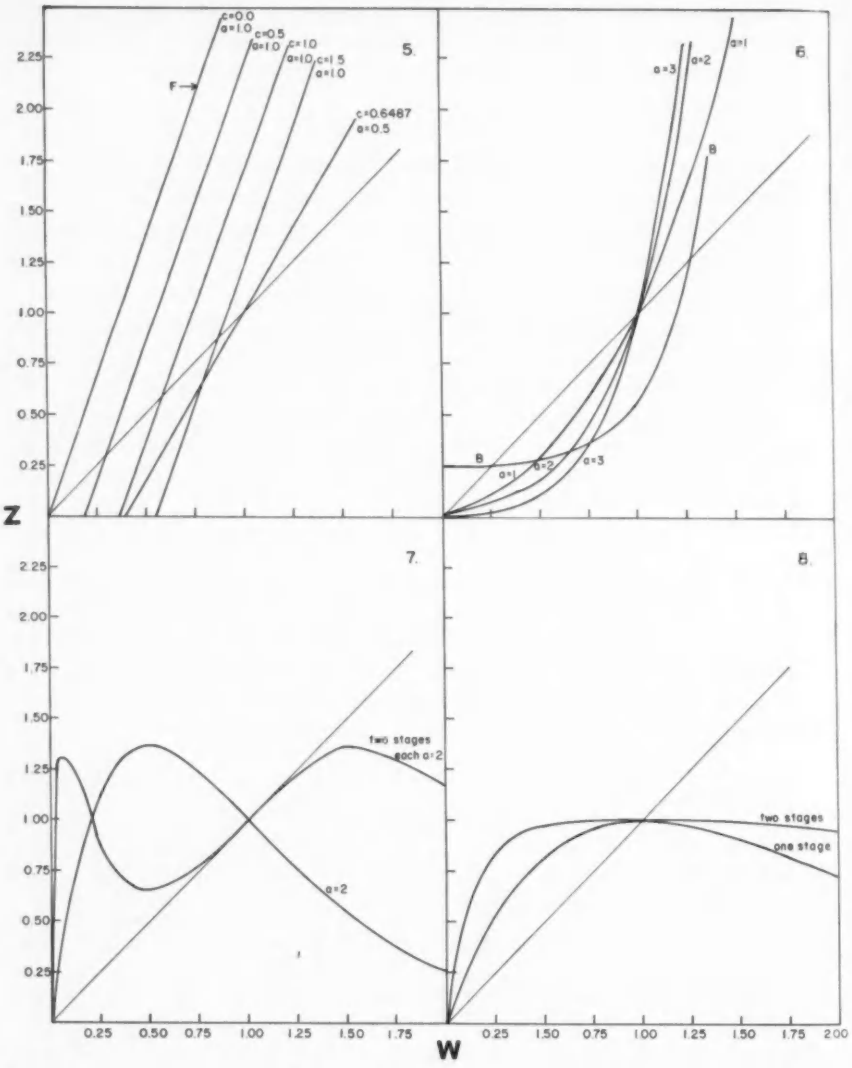

FIG. 5. Depensation curves of the general formula $Z = we^{a-bw} - C$ which represent the types of reproduction curves which would result from fixed number and/or fixed percentage predation.

FIG. 6. Curvilinear depensation expressed in the stock–recruit relationship $Z = we^{a(w-1)}$. Curve B has the added constant $R = 0.25$ and $a = 3$.

FIG. 7. Reproduction curve resulting from a two-stage life history in which the relation between input and output at each stage is given by $Z = we^{a(1-w)}$, where $a = 2$. The simple one-stage reproduction curve for $a = 2$ is given for comparison.

FIG. 8. Reproduction curves resulting from a two-stage life history in each stage of which $Z = we^{a(1-w)}$ where $a = 1$. The simple one-stage reproduction curve is given for comparison.

density. An obvious choice for a curvilinear depensation process that would result in a stock–recruit relationship that would go through the origin is

$$Z = we^{a(w-1)}. \tag{8}$$

This formula is the converse of Ricker's compensation process. It also solves to give $Z = 1$ when $w = 1$, an advantage when dealing in units of stock. Figure 6 gives some examples of curves of this group. An unlikely feature is the exaggerated benefit which large stock sizes gain from depensation, which is easily rectified by supposing that there is no depensation beyond one unit of stock.

It might also be supposed that at densities of prey *below* a certain threshold, no prey would be taken by predators, simulating for example, a refuge for a certain number of stock units of prey. This type of situation, expressed in terms of its consequences to a stock–recruit relationship, is given by

$$\begin{aligned} Z &= R + (f_1)\,(w - R) && w > R \\ &= (f_2)w && w < R \end{aligned} \tag{9}$$

where the function f_1 of w could conform to Type A predation (thus eating the surplus or a fixed number whichever is least); Type B predation (eating a fixed fraction above a threshold) or to the curvilinear depensation process represented in equation (7), i.e.

$$\begin{aligned} Z &= R + (w - R)e^{a(w-R-1} && w > R \\ &= (f_2)w && w < R. \end{aligned} \tag{10}$$

A curve of this type is given by curve B, Fig. 6, using $a = 3$ and $Z = R$ below $w = 0.25$.

LIFE-HISTORY STANZAS

The life history of many species of animals may conveniently be divided into stanzas within which compensatory or depensatory types of mortality may be characteristic. Although it can be deduced that a population can only be in equilibrium in the long term when there is an overall compensatory reproductive curve, it is nevertheless likely that this compensation is a consequence of various kinds of processes at different life-history stages. Accordingly, it seems appropriate to construct for each convenient segment of the life history a curve relating input to output which describes compensatory, depensatory or more complex kinds of effects.

Figure 7 is a simple example, representing the type of reproduction curve that results from a two-stage life history, with compensation according to the familiar form

$$Z = we^{a(1-w)}$$

with $a = 2$ in *each* stage. This kind of curve can be constructed very simply by calculating, say, Z_1 for a given w_1, then using this value of Z_1 for w_2 in the imagined second stage. The final Z_2 is then plotted against w_1 to give a reproduction curve relating parents to adult progeny of the generation. In this type of system, maximum production results from either a small or quite

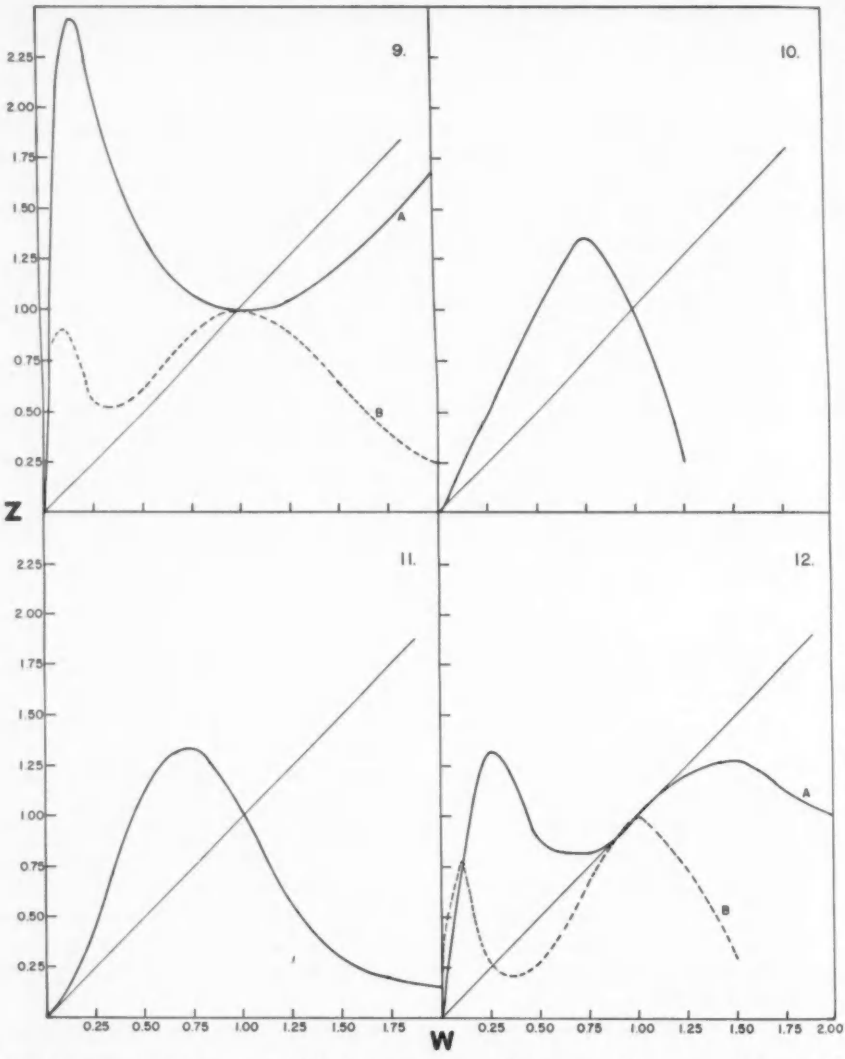

FIG. 9. Reproduction curves resulting from a two-stage life history, with compensation in each stage according to $Z = we^{a(1-w)}$. Curve A, a = 1, 3, Curve B, a = 3, 1.

FIG. 10. Reproduction curve resulting from a two-stage life history, with depensation in the first stage, $Z = we^{a(w-1)}$ where a = 2.0 and compensation in the second stage, $Z = we^{a(1-w)}$ where a = 2.0.

FIG. 11. Reproduction curve resulting from a two-stage life history with compensation ($Z = we^{a(1-w)}$, a = 1.5) preceding depensation ($Z = we^{a(w-1)}$, a = 2.0).

FIG. 12. Reproduction curves based on three life-history stages. A. Two stages each with compensation with a = 1.5, one stage of depensation a = 2.0. B. Two stages of compensation with a = 3,1, one stage of depensation a = 2.0.

substantial stock, with a dip between reflecting the compensation in the second life-history stage.

The two-stage reproduction curve where $a = 1$ (Fig. 8) is similar in form to the curve for the quotient relationship of Beverton and Holt (1957), suggesting the possibility that two moderate compensations could have the effect of making recruitment relatively constant over a wide range of stock densities.

Where the value of a is large in the second stage of a two-stage compensation process, the resultant curve may imply the unlikely situation where very small or very large stocks give the greatest recruitments (Fig. 9A). In the more plausible case where the most severe compensation occurs in the first life-history stage, the resultant of two-stage compensation also shows two peaks, with greater production resulting from the larger stock (Fig. 9B).

Two-stage reproduction curves may also be constructed so that one stage is a depensation process. Figure 10 shows the resultant of a two-stage process, the first stage of which is the depensation curve

$$Z = we^{a(w-1)}$$

where $a = 2.0$ and the second stage of which is compensation with $a = 2.0$. Figure 11 shows a two-stage process in which compensation precedes depensation. The resultant curve exhibits some similar properties to the curve G of Ricker (1958a).

Three-stage reproduction curves, though constructed to parallel what seem to be reasonable circumstances, may result in rather bizarre representations of population events. Curve A of Fig. 12 describes a population which would respond only slightly to moderate displacement from equilibrium, but would increase beyond unit stock size if reduced to 0.25 unit. Curve B is quite unrealistic, representing a stock which would oscillate about a low level, never achieving unit stock size if ever displaced therefrom.

DISCUSSION

In discussing various deviations from the compensation type of reproductive curve of equation (1), Ricker (1958b) indicated the possibilities for considerable variety in stock–recruit relationships. In each instance it was implied that a mechanism operating at some particular stage of the life history might be responsible for the characteristic shape of the reproduction curve.

Where several different life-history stages are characterized by a potential for influencing the numerical output depending on the size of the input, there are still further opportunities for modifying stock–recruit relations summarizing the whole life cycle. An example of a reproductive curve involving a three-stage life-history process, in which the first stage is compensatory, the second depensatory and the third extrapensatory, is described in Ward and Larkin (MS, 1963) in a model depicting cyclic dominance in the Adams River race of sockeye salmon.

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Tributary Homing of Sockeye Salmon at Brooks and Karluk Lakes, Alaska[1]

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ABSTRACT

The degree of preference of sockeye salmon (*Oncorhynchus nerka*) for spawning in specific tributaries to Brooks and Karluk Lakes, Alaska, was studied in 1960 and 1961. Adult sockeye salmon begin to congregate around stream mouths soon after entering these lakes. At Brooks Lake, groups of fish were seined from various stream mouths and marked with distinctive tag color combinations. One group of tagged fish from each seine haul was released back into the original donor congregation as a control, and one or more groups were transported and released into congregations around other tributary mouths. Strength of tributary preference was determined by comparing the number of fish from each group distributed on the various spawning grounds. Eighty-three per cent of the 958 fish tagged were recovered at weirs and on stream and lake surveys. Distribution to spawning areas of sockeye salmon in control and transported groups was virtually identical. The study at Brooks Lake was followed by a study at Karluk Lake to explore further the strength of tributary preference. Very few sockeye salmon experimentally prevented from entering their preferred tributary chose an alternative spawning area. Most continued to attempt to enter their blocked tributary until death. A final study at Karluk Lake confirmed the fact that sockeye salmon entering the lake were predisposed to spawn in a particular tributary and could not be conditioned to enter an alternative tributary. We conclude that sockeye salmon are indeed homing to particular tributaries in these small lakes. The biological and management implications of these findings are discussed.

INTRODUCTION

Salmon literature strongly suggests that salmon home to large rivers and lake systems. Many of our present management techniques are based on this premise. This premise was seriously challenged many years ago by Huntsman (1937) and defended in rebuttal by many fishery scientists in three articles in a Pacific Coast fisheries trade magazine in 1937 (Anon., 1937a, b; Foerster, 1937). Recently, further evidence that discrete stocks of salmonids home to specific spawning areas within a major system has been obtained. Lindsey *et al.* (1959) clipped fins on young rainbow trout entering Loon Lake, B.C., from inlet and outlet spawning streams. About 94% of the trout returning as spawners homed to their parent streams. Stuart (1957) marked 2303 brown trout from spawning runs into six streams entering Dunalastair Reservoir, Scotland, over a 3-year period, 1952–54. Only 1 fish of the 709 recaptures in subsequent spawning runs did not return to its home stream; actually, this fish had homed successfully in 1953 and 1954 before being captured in another stream in 1955. Ricker (MS, 1959) suggests that salmon home not only to major river and lake systems but

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even to tributaries. Barnaby (1943) stated his opinion that "Under natural conditions, an extremely high percentage of the fish [salmon] returning to spawn proceed to the same area where they emerged from the spawning gravel as fry." Even as early as 1918, Gilbert (1919, 1920) began recognizing certain local sockeye salmon spawning groups in the Fraser River system, for instance, the Harrison Rapids group which is characterized by lack of any significant freshwater residency as young before they migrate to salt water. Schaefer (1951) stated that "The various groups of sockeye in the Harrison River system form one of the classic examples of racial differentiation of salmonid fishes."

Two types of evidence at Brooks and Karluk Lakes in Alaska (Fig. 1 and 2) suggest that here also salmonids are homing to specific spawning areas.

Several different types of spawning grounds exist within the lakes studied. Sockeye salmon spawn in tributary streams, along lake beaches, and in the outlets of both lakes. Some areas are occupied early in the season, some during mid season, and others late in the season. This pattern of specific area occupation follows the same time and location sequence within a few days year after year. Spawning runs of sockeye salmon appear then to be separated at least into gross groups at both lakes by time and by physical distance. Thus, different tributary and outlet spawners possibly represent discrete stocks.

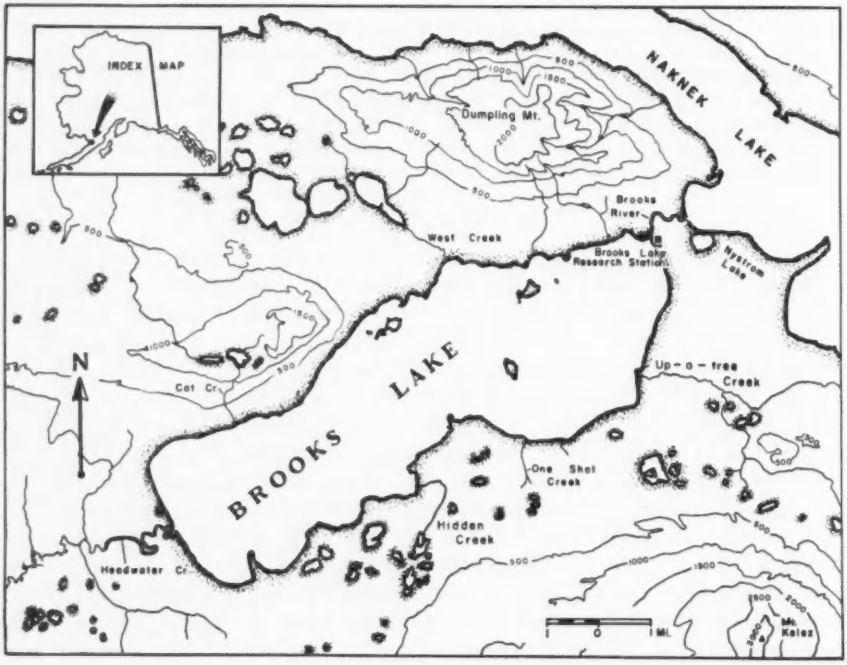

FIG. 1. Brooks Lake, Alaska, showing major sockeye salmon spawning tributaries and the outlet, Brooks River.

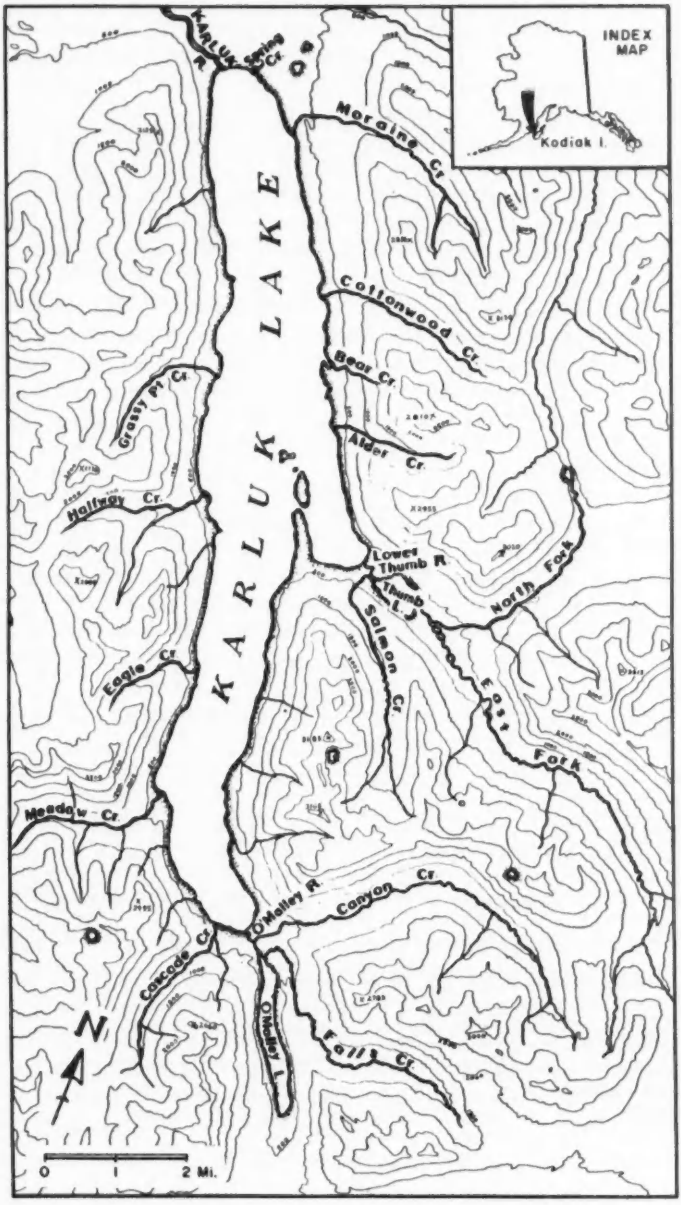

FIG. 2. Karluk Lake, Alaska, showing major sockeye salmon spawning tributaries and the outlet, Karluk River.

During 1959, length measurements were taken from spawning female sockeye salmon occupying 13 lateral streams tributary to Karluk Lake at the same time of the season. Significant differences at the 95% confidence level in mean lengths among streams with similar physical characteristics suggest that spawning stocks were apparently homing to specific tributaries.

With this background knowledge, we studied homing by sockeye salmon at Brooks and Karluk Lakes in 1960 and at Karluk Lake in 1961. Our major objective was to determine the discreteness, if any, of sockeye salmon stocks by examining the degree of preference to spawn in particular areas. Studies at Brooks and Karluk Lakes dealt with three problems related to this objective: Do sockeye salmon orient to particular spawning tributaries in small lake systems? If so, how tenacious is this preference? Finally, are sockeye salmon homing for particular spawning tributaries and beaches when they enter the lakes, or are they conditioned to particular tributaries after they reach the lakes? The findings of these studies and their biological and management implications are discussed in this paper.

BROOKS LAKE EXPERIMENTS

Experimental Design

Adult sockeye salmon begin to congregate around the mouths of Brooks Lake tributaries and Brooks Lake outlet soon after entering the lake. This congregation occurs during the period of maturation just before they enter the tributaries to spawn. In the Brooks Lake study, samples of these fish were seined, and random groups from each sample were marked with distinctive tag combinations. One group was released into the original donor congregation as a control; the other group, into congregations near other spawning areas. Tributary preference was determined by analyzing the distribution to the various spawning areas of fish from each group. The salient comparisons of recoveries are between control and distributed groups of fish.

Methods

Samples of 100 to 200 sockeye salmon were seined from congregations at the mouths of three tributaries, Up-a-tree, One Shot, and Hidden Creeks, and also at the outlet of Brooks Lake, Brooks River (Fig. 1). Certain features of these and of two Karluk Lake streams are given in Table I. Fish used in the

Table I. General features of sockeye salmon spawning tributaries at Brooks and Karluk Lakes, Alaska.

Stream	Length suitable for spawning	Average width spawning area	Average water depth	Average flow June–August
Brooks Lake	*miles*	*feet*	*inches*	*cfs*
Up-a-tree Creek	6	15	12	15
One Shot Creek	4	12	10	12
Hidden Creek	2	10	12	11
Brooks River	1	120	30	350
Karluk Lake				
Meadow Creek	½	14	10	13
Grassy Point Creek	½	12	10	12

control and the distributed-fish groups were captured and handled in the same way. Dip net loads of seined fish were placed alternately into two holding nets and were removed alternately from each holding net for tagging, regardless of sex.

Fish marked for redistribution were transported by boat in large tubs as rapidly as possible with frequent changes of water. Fish in the same experiment marked for release at the donor site were released at the time that redistributed fish were released.

The spawning destination of tagged fish was determined by the operation of weirs on Hidden Creek and Brooks River and by stream and lake beach surveys on the other known spawning grounds. The weir on Brooks River is at the lake outlet.

Twenty-two combinations of different colors and sizes of Petersen disk tags were used, and 985 fish were tagged. These 22 combinations comprised 8 experiments, each containing at least 2 groups. All fish in each group in a particular experiment came from the same seine haul. Tagging and recovery data for each group of sockeye salmon tagged in the Brooks Lake experiments are given in Table II.

Of the 985 fish released, 817 or about 83% were observed subsequently (Table II). Observers at the fish weirs counted 227 tags at Hidden Creek and 334 at Brooks River. The remaining 256 tags were counted on stream and lake beach surveys of all known spawning areas. Because fish from the same experimental group with identical tag combinations could not be distinguished on repeat surveys, recoveries of a particular tag combination equal the highest count obtained on any one survey at a particular stream and are not the cumulative count over several surveys. This fact combined with the virtually 100% recovery of tagged fish entering weired areas and the survey difficulties on large and turbid Headwater Creek must account for the range of per cent recoveries from 52 to 100. Surveys were made on foot on three of the unweired tributaries, One-Shot, Up-a-tree, and Headwater Creeks, and by boat along the lake beach spawning areas. Four tagged fish were recovered in gill nets around the mouth of West Creek (Fig. 1).

Mortality from tagging was negligible, as evidenced by generally high recovery. All fish in Groups 2, 3, 8, and 11 were accounted for (Table II), and more than 90% in Groups 10, 16, 17, 18, and 22.

Tagged fish were apparently not delayed in occupying the spawning grounds. Tagged to untagged fish ratios among spawners in Up-a-tree Creek, One Shot Creek, and Hidden Creek did not shift throughout the spawning season but remained constant.

Finally, tagging did not seem to affect the spawning behaviour of salmon. Tagged males spawned with untagged females, and tagged females with untagged males. Tagged males often attended untagged pairs, and in at least two instances, both members of a spawning pair were tagged.

TABLE II. Data on catching, tagging, and recovering sockeye salmon in the Brooks Lake experiments, 1960.

Experiment no.	Group no.	Captured		No. tagged	Tag color combination[a]	Released		No. tagged and released	No. recovered on:							Total recovered	
		Date	Site			Date	Site		Brooks River	Up-a-tree Creek	One Shot Creek	Hidden Creek	Headwater Creek	West Creek	Lake beach	No.	%
1	1	July 23	Brooks River	50	Y-Y	July 23	Up-a-tree Creek	50	39					2		41	82
1	2[b]	July 23	Brooks River	17	Y-W	July 23	Brooks River	17	17[c]							17	100
2	3[b]	July 27	Brooks River	49	Y-R	July 27	Brooks River	49	48[d]					1		49	100
2	4	July 27	Brooks River	50	Y-B	July 27	One Shot Creek	50	39							39	78
2	5	July 27	Brooks River	50	W-Y	July 27	Up-a-tree Creek	50	39	1					1	41	82
3	6	July 28	Up-a-tree Creek	49	R-Y	July 28	Hidden Creek	49	1	34		1				36	74
3	7[b]	July 28	Up-a-tree Creek	50	W-R	July 28	Up-a-tree Creek	50		42	1		1			44	88
3	8	July 28	Up-a-tree Creek	25	R-W	July 28	Brooks River	25		24		1				25	100
3	9	July 28	Up-a-tree Creek	50	B-Y	July 29	One Shot Creek	50		35	1		1			37	74
4	10	Aug. 1	Hidden Creek	50	R-R	Aug. 1	One Shot Creek	50	1			45				46	92
4	11[b]	Aug. 1	Hidden Creek	50	B-W	Aug. 1	Hidden Creek	50	1	1		48				50	100
5	12	Aug. 2	One Shot Creek	50	B-R	Aug. 2	Up-a-tree Creek	50	1	15	17	3				36	72
5	13[b]	Aug. 2	One Shot Creek	50	R-B	Aug. 2	One Shot Creek	50	1	12	17	2				32	64
6	14	Aug. 3	One Shot Creek	50	W-B	Aug. 3	Hidden Creek	50		8	14	2	2			26	52
6	15	Aug. 3	One Shot Creek	38	B-B	Aug. 3	Brooks River	38	5	4	12		2			23	61
7	16	Aug. 5	Hidden Creek	48	R-Yg	Aug. 5	Brooks River	48	4			43				47	98
7	17	Aug. 5	Hidden Creek	50	R-Yr	Aug. 5	Up-a-tree Creek	50	3			45				48	96
7	18[b]	Aug. 5	Hidden Creek	50	Yg-R	Aug. 5	Hidden Creek	50	8			37		1	2	48	96
8	19	Aug. 11	Brooks River	49	B-Yr	Aug. 11	Hidden Creek	49	34	1						35	71
8	20[b]	Aug. 11	Brooks River	50	Yr-B	Aug. 11	Brooks River	50	43				1			44	88
8	21	Aug. 11	Brooks River	40	B-Rr	Aug. 14	Midlake	40	33						1	34	85
8	22[b]	Aug. 11	Brooks River	20	Rr-B	Aug. 14	Brooks River	20	17				1		1	19	95
							Totals:	985	334	177	62	227	8	4	5	817	83

[a]Left side given first. Colors are designated R (red), Y (yellow), G (green), B (blue), and W (white). Small letter denotes small tag on top of large tag.
[b]Control experiment.
[c]Eighteen counted. Miscount at Brooks weir probably due to heavy salmon movement up and down through the weir gates at times.
[d]Fifty counted. Miscount at Brooks weir.

RESULTS

There was no prior evidence that all salmon congregating near a particular tributary or Brooks River were destined to enter that area to spawn. Thus, tests for spawning area preference involved comparing within each experiment the tag recoveries from spawners transported to other areas with those from spawners left at the capture sites as controls. The eight experiments will be discussed in their increasing order of complexity. Detailed data are given for each experiment in Table II.

Experiment 4 (Fig. 3) involved fish seined at Hidden Creek. One group of 50 was released there as a control (Group 11), and a second group of 50 was transported to and released at the mouth of One Shot Creek (Group 10) about 3 miles away. All control fish were eventually accounted for on spawning areas, and all but two spawned in Hidden Creek. Forty-six of the fish transported to One Shot Creek were accounted for, and only one did not return to Hidden Creek to spawn. The almost complete choice by fish in both groups to spawn in Hidden Creek (93 of 96 fish recovered) suggests a strong tributary preference. Apparently the congregation around the mouth of Hidden Creek at the time of

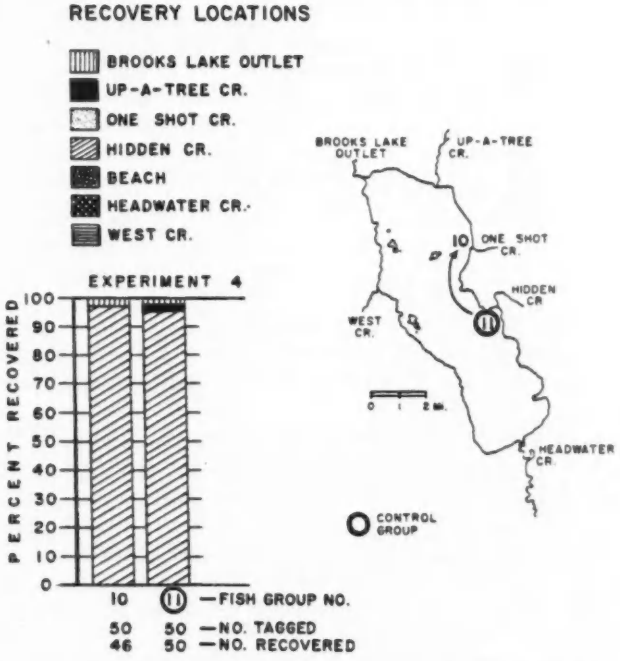

FIG. 3. Destination of adult sockeye salmon spawners in experiment 4 seined around the mouth of Hidden Creek; Group 11 was released as a control at Hidden Creek. Group 10 was transported and released at One Shot Creek.

seining was essentially homogeneous, consisting primarily of fish destined to spawn in Hidden Creek.

Experiment 7 (Fig. 4) consisted of two distributed-fish groups and one control group, and Experiment 3 (Fig. 5) consisted of three distributed-fish groups and one control group. The highly similar distribution in the spawning areas of fish from the control and distributed groups within each experiment again reflects strong tributary preference. It also appears that both congregations at the time of seining were essentially homogeneous since most fish spawned in the creek near where they were first captured.

In Experiments 1, 2, and 8 (Fig. 6–8) almost all of the fish either stayed in the outlet area (Brooks River) or returned there to spawn, indicating that the congregation at the outlet was virtually homogeneous. Results from all three experiments again demonstrate the strong preference of sockeye salmon for a particular tributary stream.

In Experiment 8 (Fig. 8) individual fish in Group 21 were distributed at 200- to 300-yard intervals down the middle of Brooks Lake to prevent schooling immediately after release. This group and its control, Group 22, were kept in

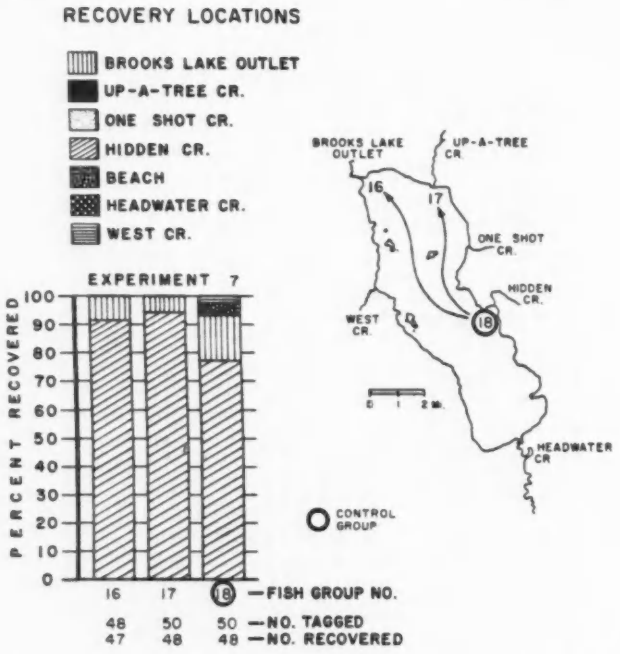

FIG. 4. Destination of adult sockeye salmon spawners in experiment 7 seined around the mouth of Hidden Creek. Group 18 was released as a control at Hidden Creek. Group 17 was transported and released at Up-a-tree Creek. Group 16 was transported and released at Brooks River.

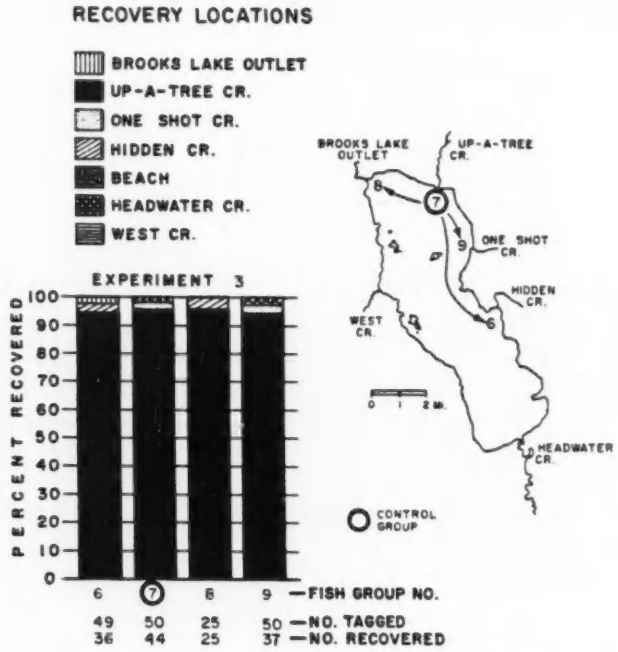

FIG. 5. Destination of adult sockeye salmon spawners in experiment 3 seined around the mouth of Up-a-tree Creek. Group 7 was released as a control at Up-a-tree Creek. Group 8 was transported and released at Brooks River. Group 6 was transported and released at Hidden Creek. Group 9 was transported and released at One Shot Creek.

holding nets at Brooks River for 2 days before being released. Neither the scattering nor the delaying caused deviation from the behaviour shown by Groups 19 and 20 (Experiment 8) which were handled in the manner previously described.

The obvious conclusion from these experiments is that sockeye salmon have an extremely strong degree of preference for spawning in particular lake tributaries or the lake outlet. But are they conditioned to specific areas during congregation as adults around stream mouths prior to spawning, or are they homing? Two additional experiments at Brooks Lake bear directly on this point. Experiment 5 (Fig. 9) carried out at Brooks Lake showed a pattern of distribution of sockeye salmon to spawning areas different from that shown in other experiments (Fig. 3–8). In Experiment 5, two groups of fish were seined and tagged from the congregation near One Shot Creek. Group 12 was transported 2 miles to the congregation off Up-a-tree Creek, and Group 13 was left at One Shot Creek as a control. About 40% of Group 12 stayed at Up-a-tree Creek to spawn, and 48% returned to the donor stream to spawn. The control

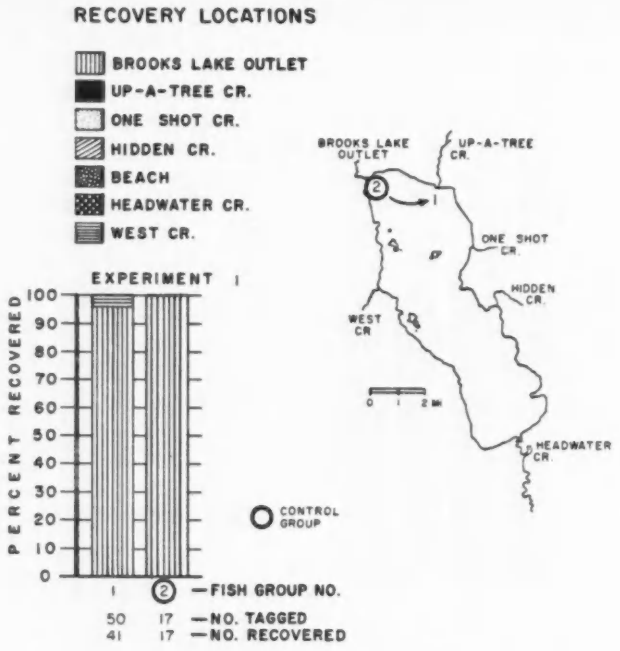

FIG. 6. Destination of adult sockeye salmon spawners in experiment 1 seined around the outlet of Brooks Lake. Group 2 was released as a control at the river. Group 1 was transported and released at Up-a-tree Creek.

(Group 13) distributed itself in about the same manner; of the control group seined off One Shot Creek and left there, 38% left the stream and migrated to Up-a-tree Creek to spawn. This evidence indicates that the belief that sockeye salmon develop a strong orientation to a tributary only after coming into its influence prior to spawning probably is incorrect. Actually, the results of Experiment 5 further substantiate the hypothesis of stock discreteness at the small tributary level. Unlike the homogeneous congregations of fish found near other spawning areas, the congregation at the mouth of One Shot Creek at the time of seining was a mixture of two major stock groups. Fish in one segment were destined to spawn in the stream near where they were schooled. Fish in the second segment, destined to spawn in Up-a-tree Creek and apparently still searching for their home stream, had stopped at the mouth of One Shot Creek. Not receiving the proper stimulus from One Shot Creek, they moved on to spawn in Up-a-tree Creek.

Experiment 6 (Fig. 10) involved two groups of fish seined at One Shot Creek the day after fish for Experiment 5 were captured. One group was transported 3 miles to Hidden Creek, the other 4 miles to Brooks River. There was no

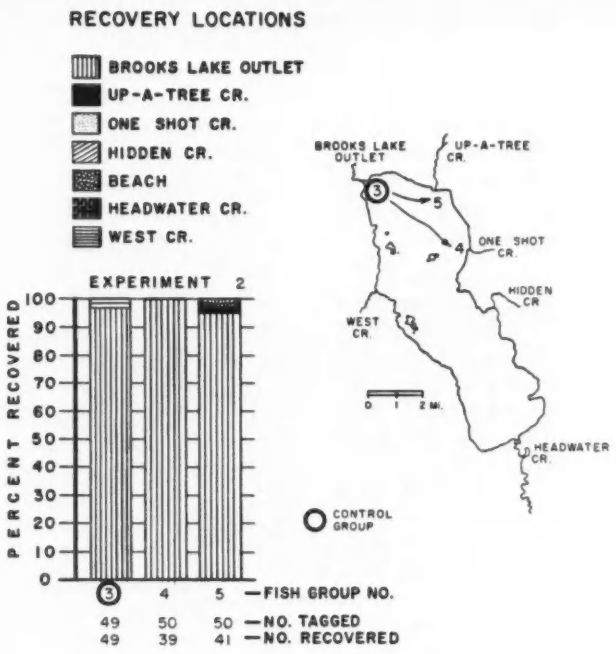

FIG. 7. Destination of adult sockeye salmon spawners in experiment 2 seined around the outlet of Brooks Lake. Group 3 was released as a control at the outlet. .Group 5 was transported and released at Up-a-tree Creek. Group 4 was transported and released at One Shot Creek.

control group in Experiment 6. As in Experiment 5 (Fig. 9), about 50% of the fish in both groups returned to spawn in One Shot Creek. Many of the remaining 50% left Hidden Creek and Brooks River and spawned in Up-a-tree Creek. The appearance of five spawners in the outlet from the group released at Brooks River and of none from the group released at Hidden Creek was considered to be sampling error related to selection of fish for each group. At least one fish each from Groups 12 and 13 released the previous day (Experiment 5; Fig. 9) spawned in Brooks River. Apparently some Brooks River fish were present in the congregation off One Shot Creek both days.

Results of Experiment 6 substantiate those of Experiment 5 in showing that sockeye salmon were homing to specific tributaries rather than developing a strong orientation to a tributary only after coming into its influence prior to spawning. In fact, fish in Experiment 6 were neither seined nor released at Up-a-tree Creek. Yet many fish migrated there to spawn. It should be pointed out here again that the comparison between the distribution of recoveries for experimental and control groups is the salient comparison. It is therefore

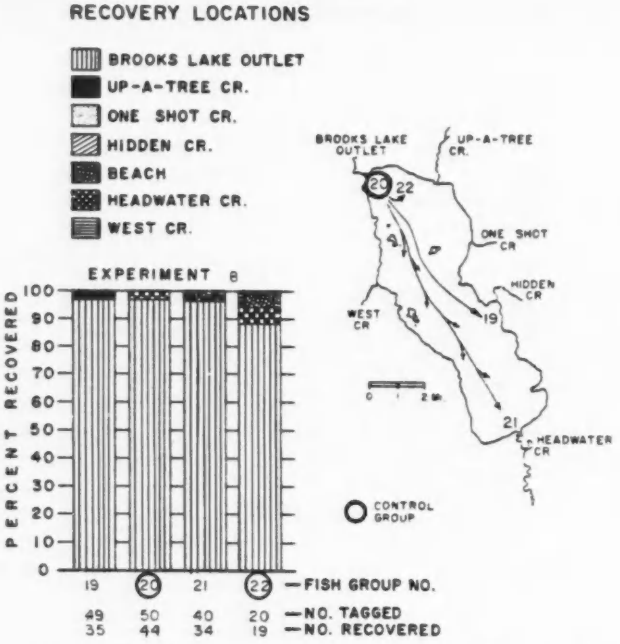

FIG. 8. Destination of adult sockeye salmon spawners in experiment 8 seined around the outlet of Brooks Lake. Groups 20 and 22 were released as controls at the outlet. Group 19 was transported and released at Hidden Creek. Fish in group 21 were scatter-released down the middle of Brooks Lake.

immaterial in the Brooks Lake studies whether the congregation of salmon from which the fish were seined was homogeneous (composed of salmon destined for one spawning area) or heterogeneous (composed of salmon destined for several spawning areas).

KARLUK LAKE EXPERIMENTS

The objective of the first Karluk Lake study was to determine the tenacity of tributary preference of sockeye salmon denied access to their preferred tributary.

In the summer of 1961 adult sockeye salmon of both sexes were captured at a weir trap as they first entered the mouth of the tributary, Meadow Creek (Fig. 2). The trapped fish were placed alternately in either an experimental or a control group. Each fish was tagged with an individual tag combination involving color, size of tag, and placement — either anterior or posterior to the dorsal fin. A group of 100 fish each from the experimental and control groups was tagged and returned to the lake. As the tagged fish entered the weir trap on subsequent attempts to enter the tributary, the individual tag combination and time and date of the attempt were recorded. Control fish that entered the

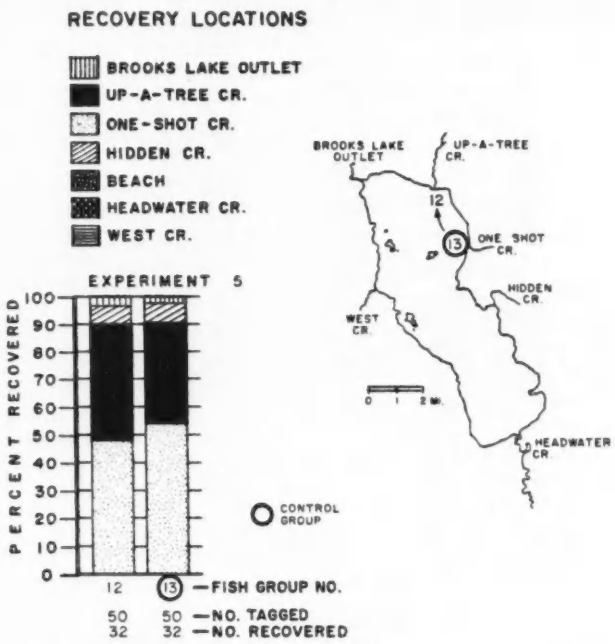

FIG. 9. Destination of adult sockeye salmon spawners in experiment 5 seined around the mouth of One Shot Creek. Group 13 was released as a control at One Shot Creek. Group 12 was transported and released at Up-a-tree Creek.

tributary were placed upstream and allowed access to the spawning beds. Experimental fish, on the other hand, were repeatedly returned to the lake. This procedure continued until tagged fish could no longer be recovered and spawning was completed within the tributary. Daily tag surveys of other spawning tributaries were conducted to record movement and utilization of these areas by individual experimental and control fish.

During this study, 99% of the control fish and 95% of the experimental fish were recovered and released one or more times (Fig. 11). After the initial release of all tagged fish back into the lake, 94% of both groups re-entered Meadow Creek, the apparent home stream, before attempting to enter any other spawning tributary (Fig. 11). Location of the last recoveries for each fish shows that 95% of the control group spawned in the apparent home stream, and 79% of the experimental group continued to attempt to enter Meadow Creek until they disappeared. Of further interest is the average of 11 attempts per experimental fish to enter Meadow Creek over the study period. Thus, the great majority of experimental fish, though completely blocked from their apparent home stream, continued re-entry attempts until disappearance and were never observed

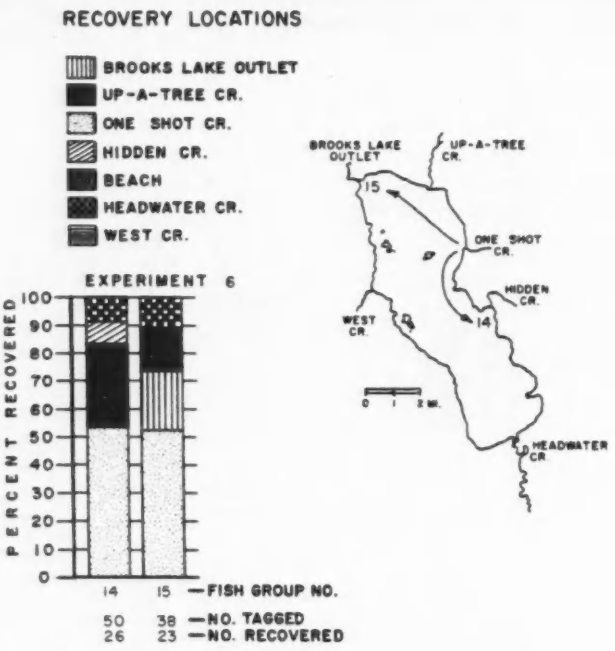

FIG. 10. Destination of adult sockeye salmon spawners in experiment 6 seined around the mouth of One Shot Creek. Group 15 was transported and released at Brooks River. Group 14 was transported and released at Hidden Creek.

on alternative spawning grounds even though observations were continued throughout the spawning period in the area of investigation.

Another study was carried out at Karluk Lake in 1961 to investigate further the possibility that fish might still become conditioned or oriented to a specific tributary after coming under its influence prior to spawning. This study entailed an attempt to influence the tributary selection of a group of salmon by holding them under the influence of a particular tributary during their lake maturation period.

Six hundred sockeye salmon adults of both sexes were captured as they first entered the lake through the Karluk weir trap and were alternately placed in three groups of 200 fish each. The control group was tagged with yellow Petersen disk tags and released. Fish from this group were expected to proceed in a normal manner to their specific spawning gravels. Their appearance on the spawning grounds would be used as a signal for releasing the two experimental groups. Fish in experimental Group 1 were tagged with red Petersen disk tags and placed in a large holding pen. Fish in experimental Group 2 were tagged with white Petersen disk tags and placed in an identical holding pen. Both holding pens were then towed up the lake halfway between the outlet and Grassy

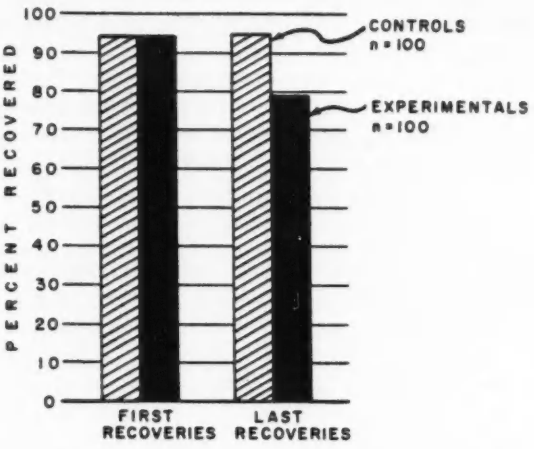

FIG. 11. First and last recoveries in Meadow Creek of tagged adult sockeye salmon in home stream preference study, Karluk Lake. Control fish were allowed free passage into Meadow Creek. Experimental fish were returned to the lake after every attempt to enter Meadow Creek.

Point tributary (Fig. 2). Fish in experimental Group 1 were then returned to the outlet of Karluk Lake and held until ready to spawn. Experimental Group 2 fish were towed to Grassy Point and held under the influence of Grassy Point Creek water during maturation. Thus, experimental Groups 1 and 2 were given the same treatment, with the exception of area of confinement. Group 1 was held under the influence of the lake outlet water rather than the water of a specific tributary.

The three groups were tagged on June 14 and 15. By late morning of June 16 both groups being retained were towed in the pens to their respective holding sites, and the holding pens were securely anchored into place. Throughout the retention period of 18 days, both pens were checked twice daily. The fish in both pens soon showed signs of abrasion from contact with the hardware cloth sides. Both groups also suffered mortality before release — 19% of experimental Group 1 and 21.5% of experimental Group 2.

On June 28 a small hole was discovered in the holding pen at Grassy Point and was repaired. Less than one dozen fish had escaped. Three of the escapees and the first of the control group fish were observed during a stream survey count of spawning adults on July 1. On July 3 both experimental groups of fish were released at their holding sites. Tagged fish from each of the three groups were recovered on subsequent weekly stream surveys from the spawning areas then being utilized. The first recoveries occurred on July 7 during the first stream survey after the release. On this date fish from all three groups were observed on the spawning beds. The last recovery was one from the control group observed 4 weeks later on August 5.

Tag recoveries at the test stream weir show that fish held at the mouth of Grassy Point Creek, experimental Group 2, did not enter that tributary to spawn in any greater frequency than fish in the other two groups. Percentage recoveries at Grassy Point were 9.1, 9.1, and 15.2 for the two experimental groups and the control group, respectively. The preference of fish in experimental Group 2 to spawn in Grassy Point Creek was not increased by the conditioning treatment.

DISCUSSION

Homing

The foregoing series of studies demonstrate: (1) sockeye salmon show a strong and tenacious specific spawning tributary preference within a small lake system, and (2) this preference is not the result of conditioning after the fish enter the lake. At Brooks Lake some fish grouped around tributary mouths did not necessarily spawn there. But the salient point is that tagged fish in groups transferred to other lake areas did ultimately spawn in the same areas and in the same proportions as did tagged fish left at capture sites as controls. At Karluk Lake most fish continued to attempt re-entry of their home tributary if prevented from doing so. Also at Karluk Lake, tributary selection of sockeye salmon was not influenced by conditioning. This cogent evidence indicates that sockeye salmon are predisposed to spawn in a particular tributary prior to entering a lake system and are indeed homing.

Searching, Overshooting, and Straying

Little is known about the routes of sockeye salmon from the time they enter Brooks and Karluk Lakes until they enter spawning areas. During this period, fish may be seen on days when the water is calm in almost any part of the lake. Fish in groups around the mouths of tributaries gradually increase in numbers during the maturation period. Such behaviour conforms to the searching and sorting process of home tributary selection discussed by Hasler and Wisby (1951).

On two occasions at Brooks Lake, fish with particular tag combinations were sighted around the mouths of tributaries other than where they were captured or released. A Y-W tagged fish in Group 2, which was seined at the outlet of Brooks Lake and left there as a control on July 23, was seen at the mouth of One Shot Creek on August 2. No Y-W tags were recovered in One Shot Creek. All fish in Group 2 eventually returned to Brooks River. Another fish seined at Hidden Creek and tagged R-R (Group 10) was released at One Shot Creek on August 1 and was seen off Up-a-tree Creek the same afternoon. No R–R tags were recovered in Up-a-tree Creek. Both of these incidents are considered to be related to the searching out of the proper stimulus by which salmon recognize their home stream.

The phenomenon of fish passing by a spawning tributary or up through a spawning area and then returning downstream to spawn may be termed "overshooting". The Y–W tagged fish from Group 2 is a specific example. Overshooting in general is demonstrated in Brooks River. Thousands of sockeye salmon that pass up through Brooks River into Brooks Lakes every year even-

tually return to spawn in the river. Some of the fish in every experiment seined around the mouths of lake tributaries eventually spawned in Brooks River, so at least some of the Brooks River fish came within the direct influence of other spawning areas and rejected them.

Finally, some evidence on the degree of straying between tributary stocks was gathered in our studies. In Experiments 1, 2, 3, 4, 7, and 8 at Brooks Lake, most fish went to one particular tributary to spawn. An average of about 6.8% of the fish chose alternative tributaries. We interpret this as representing the average maximum degree of straying between tributary stocks in Brooks Lake. Indeed, it might be quite a bit less than this, because some fish choosing alternative tributaries in the experiments may well have been homing there anyway. In the home stream rejection experiment at Karluk Lake, 5% of the control fish first entering one tributary eventually left and entered an alternative tributary; 2% ultimately returned to spawn in the first tributary. Thus, straying was actually no greater than 3%. Lindsey *et al.* (1959) found that rainbow trout, once they had spawned in the outlet of Loon Lake, B.C., almost unerringly (99.6%) returned to the outlet area to spawn for the second or third year. They also found that about 94% of the fish hatched in the outlet returned there for their first spawning. Cope (1957) found that about 97% of the cutthroat trout in Yellowstone Lake spawning a second time returned to the tributary of previous spawning. Vernon (1957) found that less than 3% of the 1131 kokanee examined in Kootenay Lake, B.C., spawned in an area in the lake other than that of their natal origin.

Biological and Management Implications

These findings reveal that each lake tributary probably supports discrete stocks or groups of stocks. Such discreteness of stocks has important biological and management implications.

Large spawning runs are likely to be complex heterogeneous assemblages of discrete stocks. The Brooks River run is only one of several important runs in the overall run of the Naknek River system. Yet, Brooks River serves as a route for stocks going to five tributaries, one beach spawning area in Brooks Lake, and Brooks River itself. The evidence suggests that every major lake tributary and beach spawning area in the entire Naknek Lake system, of which Brooks Lake is a part, may have one discrete stock or more. This same stock diversity probably holds true for the 16 spawning tributaries and several beach spawning areas in the Karluk Lake system.

Such diversity of stocks within sockeye salmon runs has long been considered probable. Thompson (1945) based his interpretation of the effect of the obstruction at Hell's Gate on the Fraser River on sockeye salmon upon the concept of races. Sockeye salmon stock diversity in the Fraser River run has been examined at three levels: upper and lower system groups (Thompson, 1945); major river groups (Killick, 1955); and major groups within one large river system, the Harrison River (Schaefer, 1951). It also seems reasonable to expect discreteness of sockeye salmon stocks down to the level of individual tributaries within each large river system.

Different interpretations of the well-known Karluk River sockeye salmon run occur in the literature. Barnaby (1943) described the run as bimodal with a spring run and a fall run that overlap to a limited extent. He observed some differences in utilization of various spawning areas by salmon in the two runs, and even where the same area was used by both spring and fall run salmon, there were great differences in time of spawning. This last feature would completely prevent breeding between spawners in different runs and suggests the existence of at least two stock groups.

Rounsefell (1958) believed that all Karluk sockeye salmon belonged to the same population or race, giving as his reasons the following: (1) the modes of abundance in the total annual run could be caused by the times when different age combinations of smolts and ocean-age fish return, and (2) significant correlations occur between fish of the same brood that return at different ages in different times of the season.

Ricker (MS, 1959) questions these two arguments. He first says that variability in abundance in a parallel fashion by different ocean groups having the same number of freshwater years " . . . might reflect variations in survival conditions in the lake during their common freshwater life." Ricker then points out that "The attempt to relate variations in numbers of spring-run and fall-run $5_{3\cdot3}$ to temperature during season of return produced only a weak and non-significant correlation (0.28)."

Owen *et al.* (MS, 1962) present new information on differences in time of spawning and place of spawning between the Karluk spring and fall runs. They discuss the possibility that discrete stocks are associated with particular spawning areas and conclude that differential fishing of the stocks may have contributed to the decline of part of the Karluk run.

The findings at Brooks and Karluk Lakes support the general contention that the run into a lake may be composed of more than one stock. Modes in the annual Karluk run (Barnaby, 1943) probably reflect the seasonal appearance of early and late spawning stocks.

Separation of sockeye salmon spawning stocks by strong homing behaviour might under certain circumstances cause some genotypic divergence. Vernon (1957) found some genotypic divergence between kokanee salmon in Kootenay Lake, B.C. He suggests that some adaptive genotypic divergence has also occurred between many sockeye salmon stocks. Vernon notes that large-scale rehabilitation programs where sockeye salmon have been transplanted to new areas even within the same river system (Foerster, 1946) have been generally unsuccessful.

Such discreteness of stocks obviously is of great significance to the fishery manager. In rehabilitation programs involving the establishment of new populations or the strengthening of weak ones by transfer of fish, adaptability of the stocks to rather local environmental conditions must be considered. In management of the fishery, or more to the point, in management of the escapement, proper numbers of spawners from each important stock must be allowed to escape. A final consideration pointed out by Thompson (1959) is that some

fish from all stocks should be allowed to escape so that the wide range of stock adaptation to varying environmental conditions can be maintained.

SUMMARY

1. At Brooks Lake in 1960, 985 adult sockeye salmon were seined from schools around stream mouths prior to the spawning period and were arbitrarily placed into 22 groups.

2. Each group was tagged with Petersen disk tags of a particular color combination. Some groups were released into their donor schools; others were released into schools around other stream mouths.

3. Eighty-three per cent of the tagged fish were recovered at weirs and on lake and stream surveys.

4. Distribution of spawning areas of tagged sockeye salmon in control and transported groups was almost identical. Thus, it was demonstrated that the sockeye salmon in Brooks Lake have an extremely strong preference to spawn in a particular tributary.

5. In 1961 at Karluk Lake, adult sockeye salmon were experimentally prevented from entering their preferred spawning tributary. Only 5% of the experimental group initially chose alternative spawning areas. Seventy-nine per cent of the fish persisted in attempting to re-enter their blocked tributary until they disappeared.

6. A final study at Karluk Lake in 1961 tested the effects of capturing adult sockeye salmon as they entered the lake and holding them within the influence of a particular tributary until the spawning period.

7. After release no more fish from this group entered that particular tributary than did fish from a group held at the lake outlet or a third group tagged and immediately released at the lake outlet.

8. We interpret these findings as follows: (1) adult sockeye salmon at Brooks and Karluk Lakes have an extremely strong preference to spawn in a particular tributary; (2) this preference is tenacious and not easily altered by experimentally blocking the entrance to the preferred stream; and (3) these fish are homing to particular spawning areas in Brooks and Karluk Lakes, and their ultimate destination cannot be significantly altered by conditioning them to a particular spawning tributary after they have entered the lake.

9. The biological and management implications of the findings are discussed.

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This manuscript is dedicated to Mr Charles Y. Conkle, recent research biologist at Karluk Lake, whose untimely death ended a promising career in fishery biology.

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The Primary Production of a British Columbia Fjord[1]

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ABSTRACT

An annual cycle of primary production was established for a British Columbia fjord. Detailed oceanographic analyses of the total oxygen budget of the fjord provided a biological oxygen budget that was further apportioned into estimations of the gross primary production (24), net primary production (24), and subeuphotic utilization of organic material. The values for 1958–59 were 671, 381, and 290 g C/m²/yr, respectively. Using C^{14} data, corrected for observed respiration and variations in insolation, 24-hr gross and net primary production estimations of 609 and 455 g C/m²/yr were derived. Over 90% of the year's primary production was attributed to the nannoplankton. The relation between the physical environmental factors of the fjord and primary production is discussed.

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FIG. 1. Oblique aerial view looking north into the mouth of Indian Arm.

1. INTRODUCTION

FJORDS present a unique environment. Their large length to breadth ratio, restricting lateral water movement, and their limited connection with adjoining waters, makes it possible to analyze many marine problems that would be impractical to attempt in the open sea. One of the more intriguing problems in biological oceanography today is the character of the annual cycle of primary production in natural bodies of waters, and its relation to environmental parameters. In most marine environments it is difficult to estimate the primary production of a body of water because suitable boundary conditions are usually lacking. However, the restriction on lateral movement of properties imposed by fjord physiography and the limited connection with adjoining waters, makes it possible to analyze the entire fjord as a biological oceanographic unit. The assessment of the primary production of a fjord, in addition to detailing one aspect of fjord biology, also presents the opportunity to assess this primary production in relation to oceanographic factors.

The primary objectives of this study were: (i) to establish the yearly cycle of primary production of a typical British Columbia fjord, (ii) to ascertain the yearly cycle of changes in the physical oceanography, and (iii) to relate these changes to concurrent changes in primary production. In order to achieve these objectives, a 3-year program was conducted consisting of 35 week-long cruises. An analysis of the annual cyclic changes in the physical oceanography of the fjord has been previously presented (Gilmartin, 1962). This paper considers the yearly cycle of primary production in the fjord, and its relation to the physical oceanography.

2. PHYSICAL ENVIRONMENT

2.1. PHYSIOGRAPHY

Indian Arm (Fig. 1) extends almost due north from a point at Lat. 49°18′10″ N and Long. 122°56′20″ W, some 15 km (1 km = .6214 mile) NE of Vancouver, British Columbia. The total length is approximately 22 km; the average width is slightly over 1 km. In common with most fjords it has a deep basin occupying $\frac{3}{4}$ of its length (Fig. 2). This shoals southward to a sill 26 m deep at the mouth, and northward into the delta of the Indian River. The fjord sides rise precipitously from a slightly concave basin floor to mountainous heights of up to 1500 m, with an average slope of approximately 40°.

2.2. CIRCULATION

The driving force for circulation in Indian Arm is the influx of fresh water from the Indian River and peripheral streams. Accumulation of this less dense water at the head of the fjord induces a seaward movement of the surface layer, with resulting entrainment of portions of the underlying water mass. Continuity considerations thus require that there be a compensating movement of water into the fjord at some sub-surface depth. The circulation pattern therefore can be resolved into a two-layer system, with net outflow at the surface and net inflow at an intermediate depth.

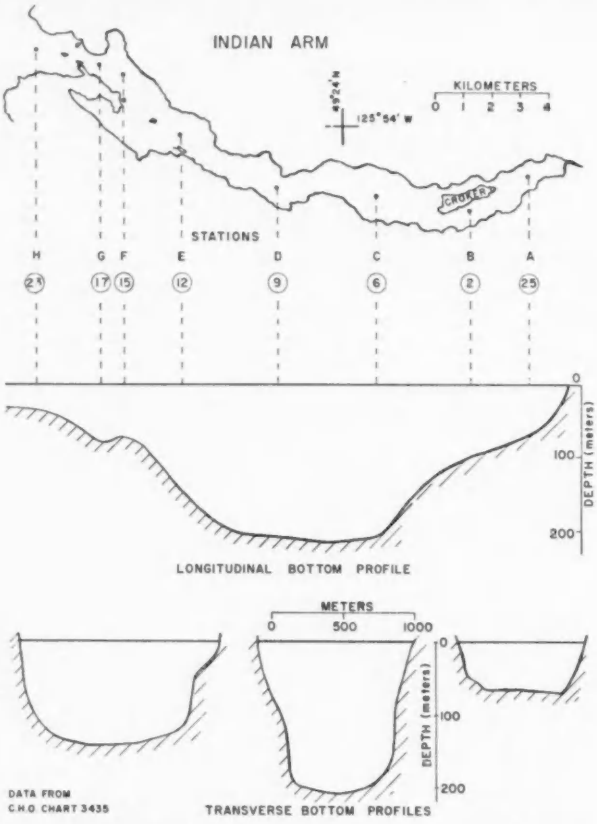

FIG. 2. Plan of Indian Arm showing station positions and longitudinal and transverse bottom profiles.

2.3. DISTRIBUTION OF OCEANOGRAPHIC PROPERTIES

The oceanography of the fjord is dominated by one basic factor: interchange of water between the fjord and the adjoining water mass is restricted to depths at or above the sill. If conditions in the adjoining water mass were constant, the distribution of conservative properties would be essentially uniform and constant from sill depth to the bottom of the basin, and would be similar to those existing at sill depth in the adjoining water mass. Above sill depth they would be continuous with those of adjoining waters.

Departure from this basic pattern is primarily due to two kinematic features: fluctuating fresh water inflow producing variations in the seaward transport of surface water, and the great variability of properties in the adjoining water mass. These variations occur on many different time scales, ranging from diurnal periods to periods up to several years. The inflow of adjoining sea water with

varying properties, and its subsequent mixing, produces the major changes in the conservative properties of the fjord basin water mass.

a. SALINITY

The fjord is a positive estuary where precipitation and freshwater inflow exceed evaporation, with the freshwater inflow presenting a characteristic annual cycle. This cycle shows a maximum in May–June, a minimum in August, a second maximum in November–December followed by a second minimum in February–March. The first maximum results from the melting of snow and ice that have accumulated over the winter; the second maximum results from the heavy autumn rains of the region. The outflow of this fresh water, with associated entrainment of underlying salt water, produces a horizontal distribution of salinity in the upper layer that usually shows a gradual increase in salinity with distance from the head.

Vertically, the salinity distribution is characterized by a distinct two-layer system: a thin brackish surface layer (0.5–5 m) showing extreme variations, and a relatively stable water mass in the basin. Temporal and spatial variations in the surface layer result from the fluctuations in fresh water discharge and entrainment of saline basin water. The deep basin is influenced primarily by the occasional intrusions of relatively high-salinity water from outside the fjord.

The main basin water mass ranges in salinity from 25 to 27‰, values 2–3‰ lower than in similar waters in the Strait of Georgia. The upper brackish layer ranges in salinity from values approaching 1‰ just off the delta of the Indian River to 25‰ at the mouth of the fjord.

b. TEMPERATURE

The vertical temperature distribution of Indian Arm also suggests a two-layer system similar to that previously noted for salinity: a thin surface layer with widely fluctuating temperatures, and a deep thick layer with substantially constant temperatures. The thin surface layer is influenced primarily by insolation and secondarily by the inflow of cold fresh water. The temperature of the deep water mass is influenced by intrusions of water from outside the fjord and by the vertical transfer of heat. This transfer produces seasonal effects discernible at depths to 125 m.

The temperature distribution presents three distinct relations between the surface layer and the deeper waters. In late summer and early fall (between the periods of maximum fresh water discharge and during the period of maximum insolation) a characteristic vertical distribution reveals a surface layer of warm water 10–16°C, which usually reaches a depth of 30 m. The lower boundary of this warm water layer is marked by a thermocline, and temperatures of 6–8°C characterize the underlying water mass. Within this mass, temperatures decrease gradually with depth, the total change being about 2 C°.

During the late fall and winter, runoff is combined with a marked decrease in insolation. The resulting vertical temperature distribution is characterized by cold surface waters with temperatures of 5–7°C, separated by a thermocline from warmer deep water with temperatures of 6–8°C. As with the previous

temperature distribution, these temperatures decrease gradually with depth. However, the coldest bottom water is always warmer than the surface water.

During spring, with increasing insolation and low freshwater discharge, the cold surface layer gradually warms until the vertical temperature distribution throughout the water column is temporarily isothermal. As a result of continued warming, the late-summer and early-fall temperature distribution again forms. The large spring runoff temporarily alters this change, particularly at the head of the fjord. At this time a shallow surface layer, colder than the underlying water mass, develops and persists for several weeks.

c. DISSOLVED OXYGEN

The distribution of dissolved oxygen, which is a non-conservative property, differs from the conservative properties (Gilmartin, 1962) since such oxygen is strongly influenced by biological activity. Thus both biological (photosynthesis and respiration) and non-biological (water movements and diffusion across the water surface) factors combine to establish the seasonal cycle.

The oxygen distribution in Indian Arm is characterized by high surface values, which at times reach 150% saturation and exceptionally as high as 250%. These decrease rapidly with depth to the approximate region of the halocline, and then more slowly to the bottom of the fjord. The relatively stable bottom waters have saturation values ranging from 10 to 30%. Here, the oxygen concentration is determined chiefly by the non-seasonal replacement pattern with intervening reduction by respiratory oxidation. The surface layers show one marked maximum during April–May–June and a second during September–October. Seasonally, these coincide with phytoplankton concentrations reported from other temperate coastal regions.

A detailed analysis of the physical oceanography of the fjord (Gilmartin, 1962) indicates that the physiography and distribution of oceanographic properties in Indian Arm is comparable to that of other mainland British Columbia fjords.

3. EXPERIMENTAL APPROACH

The greatest problem in productivity research is to obtain an accurate measurement of production. It is generally accepted that primary production is the amount of organic material which is synthesized in a unit volume of water by the activity of both photosynthetic and chemosynthetic organisms in unit time. Primary production may be considered synonymous with gross plant production, since the amount of material contributed by autotrophic bacteria is probably negligible. Net plant production is the amount of material synthesized by the plant, less the amount utilized, stored, or released as extracellular metabolites by the plant.

When an *ecosystem* such as Indian Arm is considered, the terms gross and net production are used with a slightly modified meaning. Throughout this paper gross production refers to the total amount of organic material synthesized within the boundaries of the fjord in a unit time, and net production to the amount of organic material produced in excess of the total direct and respiratory oxidative requirements of the fjord.

The extremely precipitous sides of Indian Arm limit the area of substrata suitable for the growth of benthonic algae to less than 5% of the euphotic zone (Fig. 2). Since the phytoplankton occupy virtually all the euphotic zone, it is assumed that primary production originates almost entirely from the activities of the phytoplankton.

The estimate of the rate of carbon fixation in a marine environment has been approached in several ways. Estimates of production (expressed as grams of carbon fixed per unit time) have been made from measurements of the following: (1) changes in the size of the phytoplankton population; (2) *in-situ* changes in the concentration of non-conservative water properties which are correlated with the activities of the phytoplankton; (3) temperature and available radiant energy (correlated with their effects on a given photosynthetic rate); (4) the rate of photosynthesis of a sample of the phytoplankton population. Each of these methods has certain advantages.

Estimates of the population size are usually based upon a measure of the standing crop. The standing crop is an expression of the density of the population resulting from a balance between the population's growth and depletion. Accurate estimates of the standing crop are possible, but, even if successive measurements are made at short intervals over a period of time, it is difficult to relate standing crop measurements to production. A small population under favourable conditions may have a high rate of production, whereas a large population under unfavourable conditions may have a low rate of production.

Changes in the *in-situ* concentration of non-conservative water properties yield a more accurate estimate of production. Those properties most commonly used are the concentration of nutrients, the environmental pH (correlated with the utilization of CO_2), and changes in oxygen concentration. However, the observed changes within an area are dependent not only upon the biological activity, but are also related to the amount transported to and from the area (in some instances to the amounts regenerated by organisms). If an assessment of these factors is not made, the estimate of production will be incorrect. An additional difficulty arises in that changes in concentration are often extremely small and require very sensitive methods of analysis in order to establish seasonal cycles accurately.

If the photosynthetic potential of the population can be estimated, it is possible to calculate roughly the primary production from the evaluation of fluctuations in the temperature and available radiant energy. This approach is based on the concept that in a stable marine environment (where nutrients are not limiting) three factors establish the amount of primary production: the size and efficiency of the phytoplankton population; the amount of available radiant energy throughout the euphotic zone; and the temperature.

The measurement of the photosynthetic rate of a sample of the population is often assumed to be the most accurate method of determining production. Basically this method consists of placing a sample of the natural population in a culture bottle and measuring changes in the concentration of non-conservative water properties. The production of oxygen and the uptake of labeled carbon

(C^{14}) are the two processes most often studied to obtain an index of the photosynthetic rate and are discussed in detail by Strickland (1960).

However, this approach provides, in effect, an instantaneous measure of production when production is considered on an annual basis, since incubation periods rarely exceed 12 hr.

A different approach, the *in-situ* method, is based on measurements of changes in the non-conservative properties of an entire ecosystem over some appreciable period of time (weeks to months), and provides an integrated estimate of production over that period.

There are advantages to be gained from both the *in-situ* and instantaneous approaches. On the one hand, the instantaneous method provides an accurate measure of the production of a small sample of the population in an artificial environment at a particular time. However it is only by interpretation of the data in relation to the total natural population that an estimate of the production in a particular ecosystem can be obtained. Theoretically an *in-situ* estimate of production should be more accurate since the errors inherent in extrapolating data gathered in a small artificial environment to represent a large natural ecosystem are eliminated. However, the use of this approach is usually not feasible because of the difficulties in evaluating the physical and chemical processes occurring simultaneously with production in the natural environment.

In Indian Arm, production has been estimated by three methods: instantaneous measurements of the uptake of C^{14}; the *in-situ* changes in the oxygen budget of the fjord; and the effects of temperature and the available radiant energy upon the phytoplankton population. A comparison of these three methods is discussed, and the methods are evaluated separately in section 4.

4. PRIMARY PRODUCTION

4.1. *In-situ* Oxygen Changes as Related to Production

The estimate of fjord production, using *in-situ* changes in dissolved oxygen, is derived from the detailed analysis of the physical oceanography of the fjord previously reported (Gilmartin, 1962). This analysis indicates that the major factors influencing oxygen distribution are as follows:

a. *Processes which increase oxygen concentration*
   i. diffusion from air to water
   ii. photosynthesis by algae
   iii. introduction with freshwater runoff
   iv. introduction with intruding water masses from Burrard Inlet.

b. *Processes which decrease oxygen concentration*
   i. diffusion from water to air
   ii. respiration by living organisms
   iii. chemical oxidative processes
   iv. seaward transport in outflowing water.

The most effective processes which raise the oxygen level tend to occur in surface waters, whereas those which lower the oxygen level occur in deep water.

By evaluating the oxygen budget of Indian Arm and correcting for all non-biological terms, it is possible to calculate the biological oxygen budget, and thus compute the annual cycle of net fjord production.

The change in oxygen content for a small volume of water can be expressed as:

$$\frac{\delta O}{\delta t} = p - r + \left[\frac{\delta}{\delta x}\left(\frac{A_x}{\rho}\frac{\delta O}{\delta x}\right) + \frac{y}{\delta y}\left(\frac{A_y}{\rho}\frac{\delta O}{\delta y}\right) + \frac{\delta}{\delta z}\left(\frac{A_z}{\rho}\frac{\delta O}{\delta z}\right)\right] - \left[U_x \frac{\delta O}{\delta x} + U_y \frac{\delta O}{\delta y} + U_z \frac{\delta O}{\delta z}\right] \quad (1)$$

where:
- A = eddy diffusion
- U = advection velocity
- p = rate of oxygen production by photosynthetic organisms
- r = rate of oxygen utilization by direct and respiratory oxidations
- ρ = density of sea water
- t = time
- x, y, z = axes of the co-ordinate system.

This equation (1) is generally difficult to evaluate using data from most oceanic environments, since the data necessary to correct for vertical and lateral transport are usually lacking. In some cases lateral homogeneity may minimize the effects of horizontal movements, and vertical movements may be analyzed by observing changes in the vertical distribution of conservative oceanographic properties.

In most neritic environments, the complex oceanography and rapid advective–convective processes make the equation even more difficult to evaluate. An exception to this is the fjord environment. The boundary conditions established by fjord physiography normally restrict communication with the sea to one point. Hence when the changes in oxygen within the entire fjord are considered, the evaluation of advective–convective processes is primarily concerned with this one opening.

In Indian Arm, with a right-hand co-ordinate system in which x is directed along the length of the fjord, y across, and z downward, equation (1) is modified in accordance with the following considerations. The sides of the fjord allow no movement out of the fjord along the y axis ($U_y = 0$) and lateral homogeneity is assumed ($\delta 0/\delta y = 0$). Thus the A_y and U_y terms are eliminated. The boundaries established by the water surface and fjord bottom permit no movement of oxygen along the z axis except by diffusion across the air–sea interface. Upon integration through the whole volume of the fjord, the U_z term becomes zero and the A_z term takes on the value established by the upper boundary. Equation (1) is therefore reduced to:

$$\frac{\Delta O}{\Delta t} = \int \left\{ p - r + \left[\frac{\delta}{\delta x}\left(\frac{A_x}{\rho}\frac{\delta O}{\delta x}\right)\right] - \left[U_x \frac{\delta O}{\delta x}\right] + \left[\frac{\delta}{\delta z}\left(\frac{A_z}{\rho}\frac{\delta O}{\delta z}\right)\right]\right\} dv \quad (2)$$

When changes in the total amount of oxygen within the fjord are considered, the non-biological addition or subtraction of oxygen will be due to the combined A_z and U_x terms in equation (2), plus the diffusion represented by the A_z term. The changes in oxygen concentration, as will be discussed later, can be converted to changes in fixed carbon. Since the analysis of the bottom sediments (Gilmartin, 1962) indicates that little if any organic material is deposited on the bottom, the biological changes in the total oxygen of the fjord represent the production and utilization of organic material. These observed changes can therefore be converted to net fjord production by the equation:

$$\frac{\Delta C}{\Delta t} = \frac{1}{k}(P - R) + A + D \tag{3}$$

i.e.

$$\Delta C = \Delta t \left[\frac{1}{k}(P - R) + A + D \right]$$

where:

ΔC = change in the amount of fixed carbon
k = constant to convert oxygen to equivalent fixed carbon
P = amount of photosynthetically produced oxygen
R = amount of oxygen consumed by all direct and respiratory oxidative processes
A = net transport of oxygen into or out of the fjord
D = net diffusion of oxygen across the air–sea interface.

The evaluation of the oxygen budget of Indian Arm is based on monthly measurements at seven stations along the fjord. At each station the dissolved oxygen content was determined at a series of standard depths (0, 2.5, 5, 7.5, 10, 20, 30, 50, 75, 100, 150, and 200 m). It is assumed that the integrated oxygen value for the water column is representative of the entire volume of water at the station (i.e. including half the distance to each adjoining station). Summation of these values provides a measure of the entire amount of dissolved oxygen within the fjord at a given time.

The problem of estimating oxygen diffusion across the air–sea interface has been investigated by Redfield (1948). This diffusion is primarily dependent on a pressure head at the interface, established by the partial pressures of oxygen in the atmosphere and in the water. The pressure head can be considered as the oxygen saturation deficit or saturation surplus of the surface water. If this water is supersaturated, oxygen moves out into the atmosphere; if undersaturated, oxygen moves into the water. The difference in partial pressures can be expressed as:

$$P - p = 0.21\,(1 - w)\,\frac{C_o - C_x}{C_o} \tag{4}$$

where:

P = partial pressure of oxygen in the atmosphere
p = partial pressure of oxygen in the water
w = water vapour tension of the atmosphere
C_o = solubility of oxygen in the water
C_x = oxygen content of the water.

The total diffusion of oxygen across a given surface area can then be calculated as:

$$D = kE\,(P - p) \tag{5}$$

where:

D = diffusion
k = gas diffusion constant
E = surface area.

The exact value to assign for the gas diffusion constant (k) in equation (5) is open to interpretation. The only comprehensive determinations in marine environments are based on data from the northwestern Atlantic (Redfield, 1948). In this study two empirically derived constants were calculated: a summer value of 2.8×10^6 ml O_2/m^2/month/atmos, and a winter value of 13×10^6 ml O_2/m^2/month/atmos. This seasonal difference was attributed to winter conditions at the sea surface. At this time, the actual area of air–water interface present at the surface of the water column was increased, presumably as the result of winter storms with their associated waves and turbulence. Redfield calculated these values from oxygen saturation values reported by Fox (1909). When they are corrected using the saturation values reported by Truesdale *et al.* (1955), and converted to mg O_2/m^2/month/atmos, the summer value is 3.4×10^6. Since the fjord physiography provides a sheltered body of water, it is probable that conditions in the fjord more closely approximate summer than winter surface conditions in the northwestern Atlantic. Therefore the value 3.4×10^6 has been used in diffusion calculations throughout this paper.

The diffusion quantities for Indian Arm, presented in Fig. 3, have been calculated from a summation of the quantities determined at each of Stations A to F.

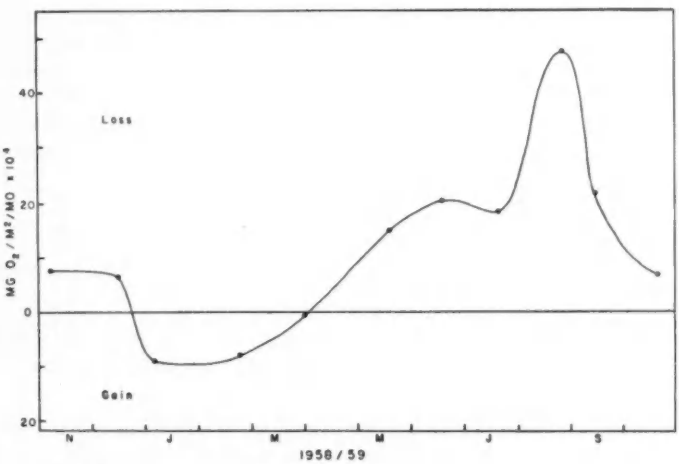

FIG. 3. Seasonal variation in the diffusion of oxygen across the air–sea interface.

TABLE I. Net transport of fjord oxygen (1958–59).

Date	T_o	T_i	T_r	$(T_i+T_r)-T_o$	T
Oct.	132.38	70.56	56.67	− 5.15	−1.33
Nov.	148.20	78.37	72.82	+ 2.99	+ .78
Dec.	270.35	145.56	126.18	+ 1.39	+ .36
Jan.	391.18	292.05	97.66	− 1.47	− .38
Feb.	269.20	202.02	51.16	−16.02	−4.15
Mar.	152.53	85.14	62.73	− 4.66	−1.21
May	104.81	47.08	34.54	−23.19	−6.01
June	188.33	113.81	59.70	−14.82	−3.84
July	128.17	74.60	27.17	−26.40	−6.84
Aug.	57.67	26.84	6.97	−23.87	−6.20
Sept.	37.64	12.43	17.09	− 8.12	−2.10

\+ = infjord.
− = outfjord.
T_o = mg O_2/sec transported out by outflowing waters $\times 10^4$.
T_i = mg O_2/sec introduced by inflowing waters $\times 10^4$.
T_r = mg O_2/sec introduced by freshwater runoff $\times 10^4$.
T = total net transport in mg O_2/month $\times 10^{11}$.

TABLE II. Net oxygen budget for fjord (1958–59).

Date	O_2	ΔO_2	t	D_1	D_2	T_1	T_2	$B\Delta O_2$	NP
21 Oct.	77.7*								
		− 1.3	.5	−15.5	− 7.75	− .27	− .1	+ 6.6	+ 10.9
7 Nov.	76.4								
		+ 6.4	1.2	+12.5	+15.0	+ .57	+ .7	− 9.3	− 15.1
15 Dec.	82.8								
		+ 6.7	.7	+14.0	+ 9.8	+ .37	+ .3	− 3.4	− 5.6
5 Jan.	89.5								
		+14.7	1.6	+15.5	+24.8	.00	.0	−10.1	− 16.7
23 Feb.	104.2								
		+ 7.4	1.2	+ 7.8	+ 9.4	−2.68	−3.2	+ 1.2	+ 2.0
31 Mar.	111.6								
		+ 5.1	1.4	−14.5	−20.3	−3.61	−5.1	+30.5	+ 50.3
11 May	116.7								
		− 7.5	1.3	−31.8	−41.3	−4.93	−6.4	+40.2	+ 66.4
19 June	109.2								
		− 3.3	1.0	−35.7	−35.7	−5.34	−5.3	+37.7	+ 62.2
20 July	105.9								
		− 9.0	1.2	−60.6	−72.7	−6.51	−7.8	+71.5	+118.0
25 Aug.	96.9								
		− 0.0	.7	−63.2	−44.2	−4.14	−2.9	+38.1	+ 62.9
14 Sept.	87.9								
		− 4.1	1.2	−25.0	−30.0	−1.77	−2.1	+28.0	+ 46.2
20 Oct.	83.8								

* = interpolated datum.
O_2 = total fjord dissolved oxygen (mg $O_2 \times 10^{11}$).
ΔO_2 = change in fjord dissolved oxygen between observations (mg $O_2 \times 10^{11}$).
t = time in months between observations.
D_1 = mean monthly diffusion (mg $O_2 \times 10^{11}$).
D_2 = monthly diffusion corrected for time between observations (mg $O_2 \times 10^{11}$).
T_1 = mean monthly transport (mg $O_2 \times 10^{11}$).
T_2 = monthly transport corrected for time between observations (mg $O_2 \times 10^{11}$).
$B\Delta O_2$ = change in fjord dissolved oxygen between observations due to biological activity (mg $O_2 \times 10^{11}$).
NP = fjord net primary production (g C/m^2).

The net advective movement of oxygen into or out of the fjord results from the oxygen introduced in freshwater runoff and inflowing deep water, less the amount transported out of the fjord in the surface layers. The total volume of runoff was estimated on the basis of adjusted river runoff data and has been previously reported (Gilmartin, 1962). The volume and depth of transport into and out of the fjord was calculated on the basis of the observed distribution of conservative properties. By relating the observed concentrations of dissolved oxygen at these depths with the volume of transport, the total net movement of oxygen into or out of the fjord was calculated. These net transport volumes are presented in Table I.

The observed changes in the total oxygen content of the fjord, corrected for advective and diffusive processes, provide an estimate of the biological oxygen budget of the fjord. The oxygen data for 1956–57 and 1957–58 are insufficient to justify this approach during these years. However, adequate data permit an estimate of the budget for 1958–59 and are presented in Table II and Fig. 4.

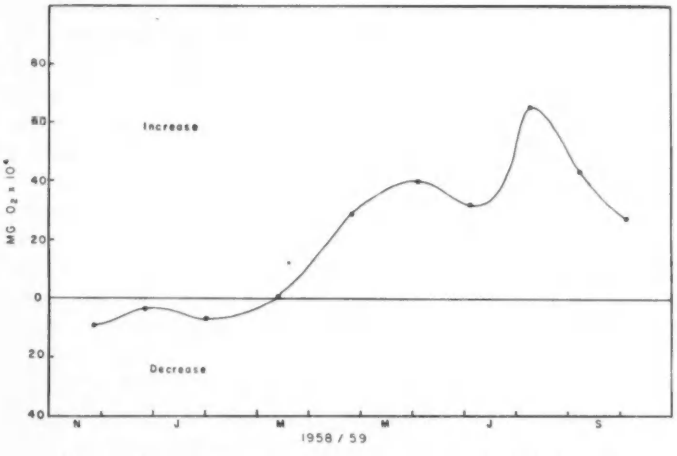

FIG. 4. Seasonal variation in the net oxygen budget of the fjord.

The factor for converting observed oxygen changes to fixed carbon (k in equation 3) is calculated as follows:

$$k = \frac{0.375}{PQ} \tag{6}$$

where: k = mg C/unit time/unit volume

$$PQ = \frac{\text{molecules of } O_2 \text{ released in photosynthesis}}{\text{molecules of } CO_2 \text{ assimilated}}.$$

The exact value of PQ has been experimentally determined over a wide range of conditions and with a variety of photosynthetic organisms (Rabinowitch, 1945,

1951, 1956; Ryther, 1956; Strickland, 1960). The reported values range from approximately 1.0 to 1.5. These values depend on several factors, including the type of material synthesized, the immediate source of available nitrogen, the light intensity and the composition of the phytoplankton population. In this study, the value of 1.2 suggested by Strickland (1960) for marine environments has been used. The net oxygen budget for the fjord has been converted to mean monthly changes in fixed carbon using equation (3). These data are presented in Table II. The algebraic sum of these changes indicate a net fjord production of 381 g C/m²/yr.

An analysis of the bottom sediments indicated that little if any organic material was deposited on the bottom. This suggests that most of the organic material produced within the euphotic zone is either transported out of the fjord or utilized by living organisms within the fjord.

A second method of applying oxygen changes to estimate production is based on the oxygen utilized during the respiratory oxidation of organic material, rather than on that produced during the photosynthetic production of organic material. If all the organic material oxidized originated within the fjord, such utilization must provide a minimal measure of the production.

During this study, 16 periods occurred when the advective processes were restricted primarily to the upper 100 m (when occurring below 100 m they were weakly developed and influenced only the most southern end of the basin). During these periods the deep-basin oxygen concentration decreased steadily with time (Gilmartin, 1962; Anon., 1956–59).

Possible errors in this approach would be introduced by any advective movements of water from outside the fjord during these periods or by vertical mixing within the fjord. Examination of the waters at sill depth outside the fjord shows that if these waters moved into the deep basin they would have oxygen concentrations higher than those present within the basin. The vertical oxygen gradient is such that any downward mixing would also introduce water with higher oxygen concentrations. Therefore both processes (if they occurred) would tend to reduce the observed rate of oxygen depletion and *make any calculated production values minimal.*

In order to relate the observed oxygen depletion to production, it is necessary to assume that the observed depletion is typical of the entire fjord. But this is not the case. While the vertical migrations of the zooplankton suggest that throughout a 24-hr period zooplankton respiration is roughly the same for the entire water column (McHardy, personal communication), the same cannot be said for bacterial and phytoplankton respiration. *A priori*, as a consequence of the density distribution, one would expect the rate of bacterial decomposition of organic material to be at a maximum somewhere in the upper 100 m of the water column. This would most likely occur in the region of a pycnocline which slowed or prevented the sinking of organic material. The heaviest concentrations of phytoplankton are found in the upper 50 m. Therefore phytoplankton respiration is probably highest in this depth range. Both of these processes suggest a higher rate of oxygen utilization in the upper 100 m of the water column than

in the basin waters. Consequently, errors introduced by assuming that the observed oxygen depletion in the deep basin is characteristic of the entire fjord make any calculated production values minimal. Thus the oxygen-utilization approach provides an estimate of the lower limit for fjord production.

The curve representing the annual cycle of oxygen utilization varies in magnitude from year to year, but it should have about the same shape each year. Thus the 16 calculated depletion values have been plotted together (Fig. 5) to establish the shape of this curve. Integration of the area under the mean curve provides an estimate of mean oxygen utilization for the 3 years.

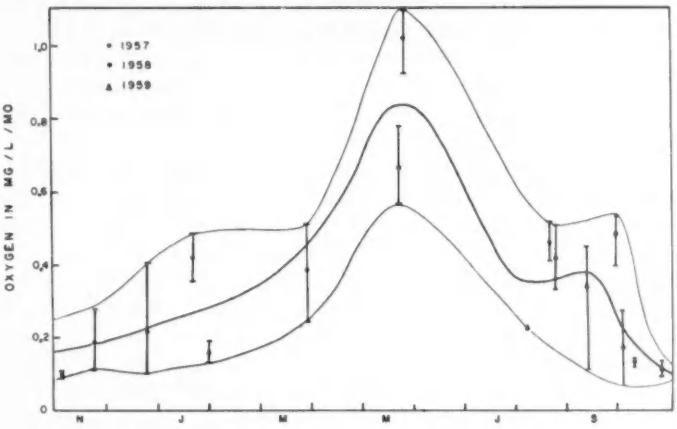

FIG. 5. Seasonal variation in oxygen utilization within the fjord

Integration of the curve areas representing the highest and lowest values provides an indication of the year-to-year variations. These values converted to fixed carbon yield a mean of 290 g C/m²/yr with extremes of 160 and 430 g C/m²/yr.

Since the oxygen-utilization and the oxygen-production approaches measure two different fractions of gross fjord production, their summation provides an estimate of the total production. The estimate of mean yearly utilization of organic material produced within the fjord was 290 g C/m²/yr. The estimated net fjord production for 1959 was 381 g C/m²/yr. Thus, if the oxygen-utilization values are representative, the gross fjord production for 1959 was 671 g C/m²/yr.

4.2. Measurement of Production by the C^{14} Method

The radiocarbon method of estimating production used in this study is based on the incubation of natural phytoplankton samples at the depth from which they were gathered. This provides a measure of the net primary production occurring under *in-situ* light and temperature conditions. It is in direct contrast to the method where samples are placed in an incubator under standard light and temperature conditions. While the latter method provides an accurate measure of the relative production of different areas it provides little information about the actual production of a specific area.

The technique of sample handling and counting, in general, follows the procedure developed by Doty (1956). In this study, samples of water with their contained phytoplankton were collected from a series of standard depths (0, 5, 8, 12, 19 and 30 m) using a Van Dorn-type plastic water bottle (Van Dorn, 1956). The samples were brought to the surface, inoculated with C^{14} and then suspended at the depths from which they were collected. In order to minimize the effects of ship shadow, the point of suspension was the end of a 6- to 8-m boom attached to the side of the ship. Usually the *in-situ* incubations were carried out from sunrise to sunset. On all but one occasion, full-day incubations were carried out at Station C or D. On this one occasion, and in certain of the supplementary incubations, the samples were incubated for half a day. In these cases, the incubations were from sunrise to local apparent noon or from local apparent noon to sunset. The results of the half-day incubations were doubled to obtain an estimate of the production that occurred during the entire day.

At the completion of the incubation the samples were filtered; first through silk net discs (least aperture dimension 56μ) to determine the relative proportion of production attributable to net plankton, and second, through Millipore filters

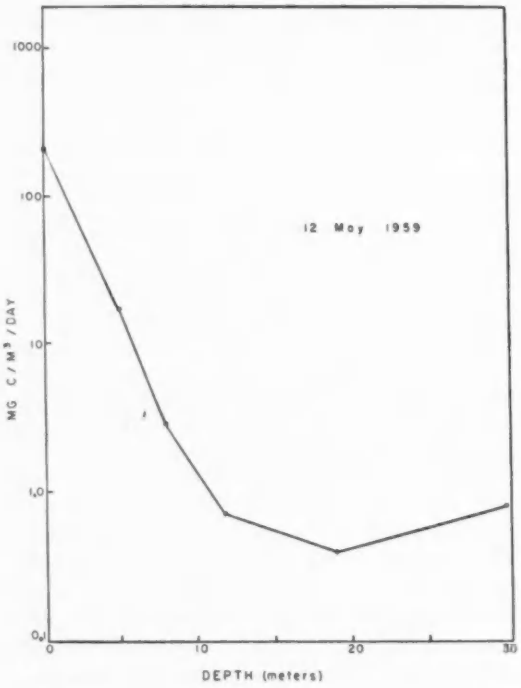

FIG. 6. Daylight C^{14} net primary production plotted as a function of depth.

(HA, pore size 0.45 μ) to determine the relative proportion attributable to nannoplankton. The silk discs and Millipore filters were subsequently counted using a gas-flow Geiger counter. The counts, corrected for isotope effect by a 1.05 factor were converted to mg C/m^3 using carbonate-carbon values calculated from salinity, temperature, and pH values by the method described by Harvey (1957). These fixed carbon values were plotted on a log–linear scale as a function of depth, and interpolated at 1-m depth intervals (see Fig. 6). A summation of these values was made to represent the net carbon fixed under 1 m^2 of the sea surface per day. These values are presented in Table III.

Depending on the particular distribution of the phytoplankton population within the fjord, the production may vary with position. Since the object was to determine the mean production of the entire estuary it was necessary to gain some measure of the relative production of the various sections of the fjord. During most cruises it was impracticable to make *in-situ* C^{14} production measurements at more than two stations. However, the use of a shipboard incubator provided a source of supplementary data. During 1959 a slightly modified version of the "Salpa tank" incubator (Doty, 1957) was used. On each cruise a series of samples was collected from the standard production depths at three stations along the fjord, and incubated under uniform light and *in-situ* temperature conditions for a period of 24 hr. The relative net photosynthesis values thus determined (by the light and dark bottle O_2 technique) were used to weight the *in-situ* C^{14} measurements of production at a particular station in order to estimate the production of the entire fjord. When time permitted more than one *in-situ* incubation, each series was corrected to provide production values for the entire fjord. Subsequently the values were averaged to provide a mean production estimate for the month. These data and calculations are presented in Table III.

One serious limitation in the C^{14} method is that it does not provide information on the amount of material respired; in addition the net production measured (Doty, 1959; Ketchum *et al.*, 1957; Menzel and Ryther, 1959) is only daylight net production. Therefore it does not yield information on gross production or on the ecologically more significant 24-hr net primary production.

During 1959 the shipboard incubator used for determining the relative photosynthetic rates of different regions of the fjord at the same time provided an estimation of the rate of respiration throughout the euphotic layers of the fjord water mass. During the year a total of 102 useable measurements were made, usually with samples collected from 0, 5, 8, and 12 m (during January, February, and March, samples were only collected from 0 m). The mean monthly values for the fjord are presented in Fig. 7. These values were subsequently weighted according to the proportion of net primary production observed at various depths throughout the euphotic zone to provide an estimate of euphotic-zone water-column respiration, and multiplied by the total area of the fjord to derive values for total fjord euphotic-zone respiration. By subtracting that fraction of the euphotic-zone respiration corresponding to nighttime respiration from the net primary production observed during the day, estimates

TABLE III. *In-situ* C^{14} measurements of net primary production corrected for relative production potential of fjord regions and adjusted to provide mean production values for Indian Arm.

Date	C^{14} *in-situ* measurements of net primary production (mg C/m²/day)				Incubator relative net primary production (mg O_2/l/24 hr)			C^{14} net primary production adjusted for relative production potential (mg C/m²/day)			Mean net primary production weighted for relative station area			Mean fjord net primary production (mg C/m²/day)
	Sta. A	Sta. C	Sta. D	Sta. E	Sta. A	Sta. C	Sta. E	Sta. A	Sta. C	Sta. E	Sta. A	Sta. C	Sta. E	
5 Nov.		295							295					
6 Nov.		477							477					
$\bar{x}$									386					386
16 Dec.		34							34					
x									34					34
6 Jan.	29								29					
7 Jan.	18								18					
x									24					24
24 Feb.	597				0.05	0.08	0.20	**373**	597	**1493**				
25 Feb.	265							**166**	265	**663**				
$\bar{x}$	270							270	431	1078	41.9	147.0	543.3	733.2
1 Apr.	226				0.45	0.20	0.22	**509**	226	**249**				
2 Apr.	1211							**2725**	1211	**1332**				
$\bar{x}$	1617								719	791	250.6	245.2	398.7	894.5
12 May			6179		0.34	1.73	3.09	**680**	**3460**	6179				
13 May	2810							**554**	2810	**5030**				
14 May	3713							**731**	3713	**6646**				
$\bar{x}$	654								3324	5947	101.4	1133.5	2997.3	4232.2
16 June	2665				0.37	0.70	0.60	**1410**	2665	**2284**				
17 June			2455					**1522**	**2872**	2455				
18 June	1961							1961	**3706**	**3177**				
$\bar{x}$	1631								3081	2639	252.8	1050.6	1330.1	2633.5
21 July	883				1.94	1.22	0.58	**1404**	883	**419**				
$\bar{x}$	1404								883	419	217.6	301.1	211.2	729.9
17 Sept.	1870				2.02	1.91	1.86	**1982**	1870	**1821**				
18 Sept.			2282					**2487**	**2350**	2282				
$\bar{x}$	2235								2110	2052	346.4	719.5	1034.2	2100.1
21 Oct.	654				3.47	2.18	1.07	**1040**	654	**321**				
$\bar{x}$	1040								654	321	161.2	223.0	161.8	546.0

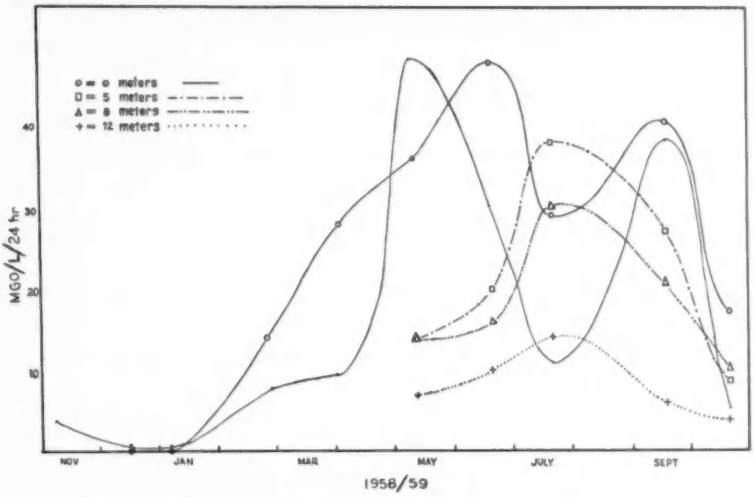

FIG. 7. Mean fjord respiration at various depths throughout the euphotic zone.

of 24-hr net primary production were derived. By adding that fraction of the respiration corresponding to the length of the day during which daylight net primary production was observed, estimates of gross primary production were derived. These data and calculations are presented in Table IV.

The chief error in this method of converting the observed C^{14} net production to 24-hr net and gross production arises in regarding the observed respiration in the incubated dark bottle as representing phytoplankton respiration alone. Actually the respiration of the bacteria and any zooplankton contained in the sample is included in the calculated "phytoplankton respiration". This error would render the calculated phytoplankton respiration too high, and the calculated 24-hr net primary production too low. Therefore this estimate of net production, while possibly in error, still provides a minimal estimate of net fjord primary production.

This method of measuring production suffers from the additional disadvantage that the observations are usually made on only one or two days at approximately monthly intervals. In order to gain an estimate of the total annual production, it would be necessary to consider these values as representative of the time interval between observations, or to adjust the values to allow for changes in the environmental factors which may influence production. The primary factors determining production are the size and efficiency of the phytoplankton population, the relationship to euphotic zone nutrients, and the availability of radiant energy. Over short-term periods, light and population efficiency are assumed to be the most important; primary production is usually approximately proportional to light energy up to certain limiting values, which are characteristic for a particular population and its physiological state. In

TABLE IV. Estimations of mean fjord net primary production corrected for respiration to provide estimations of 24-hr net primary production and gross primary production.

Date	Mean fjord net primary production (mg C/m²/day)	Depth (m)	Number observations	Mean respiration (mg O_2/l/24 hr)	Mean fjord euphotic zone respiration (mg C/m²/day (24))	Respiration net primary production	Day respiration (mg C/m²/day)	Night respiration (mg C/m²/night)	Adjusted net primary production (mg C/m²/day(24))	Adjusted gross primary production (mg C/m²/day(24))
5–6 Nov.	386		0			assumed .25	97	153	233	483
16 Dec.	34	0 5 8 12	4	0.02		assumed .25	9	20	14	43
6–7 Jan.	24	0 5 8 12	4	0.02		assumed .25	6	11	23	30
24–25 Feb.	732	0 5 8 12	4	0.14 (0.09)	244	.14	104	140	592	836
1–2 April	894	0 5 8 12	4	0.28 (0.18)	488	.23	204	284	610	1098
12–14 May	4232	0 5 8 12	5 6 4 4	0.36 0.14 0.14 0.07	593	.09	378	215	4017	4610
16–18 June	2633	0 5 8 12	6 5 4 3	0.48 0.20 0.16 0.10	705	.21	542	253	2380	3175
21 July	730	0 5 8 12	5 5 5 4	0.29 0.38 0.30 0.14	578	.52	378	200	530	1108
17–18 Sept.	2100	0 5 8 12	4 6 3 4	0.42 0.27 0.21 0.06	731	.18	381	350	1750	2481
21 Oct.		0 5 8 12	4 3 3 3	0.17 0.08 0.10 0.04	285	.22	124	161	385	670

this study, data were available on both the photosynthetic efficiency of the population and on variations in the daily total incident radiation.

The daily radiation pattern was determined from pyroheliometer measurements continually recorded in Vancouver at a point 24 km due west of the fjord mouth. If one assumes that primary production is proportional to surface radiation, and that the radiation measured is representative of Indian Arm, then it is possible to adjust the observed instantaneous C^{14} measurements of production. These adjustments would make allowance for variations occurring in the radiation pattern between monthly measurements of production. Such adjustments do not fully take into account the effects of other factors such as nutrients and temperature. These will be partially reflected in the observed production efficiency determined at the beginning and end of a particular period of time. These data and calculations are presented in Table V and Fig. 8.

The yearly cycle of gross primary production follows a bimodal curve, rising steeply from a mid-winter low during December and January to a spring maximum during May. It then tapers off slowly to a mid-summer minimum in July, rising steeply again to a fall maximum in September. In general, the net primary production cycle follows the same cycle. Daily gross production ranges from 0.03 to 4.8 g C/m²/24 hr with an annual mean of 2.2, and net production ranges from 0.01 to 3.7 g C/m²/24 hr with an annual mean of 1.4. When the production of the entire fjord is considered, net primary production ranges from a low of 35% of gross primary production during the beginning of the spring maximum in April, to a high of 85% during the latter portion of the spring maximum, with an average of 65% for the entire year. There is a tendency for the proportion of net to gross production to be lowest during periods of rapid growth (e.g. at the time of the development of the spring or fall rapid increase in population—the so called "bloom"), and to be the highest during the periods of decline. This may be associated with the phenomenon discussed by Rabinowitch (1945), who reported that respiration is markedly stimulated by the products of photosynthesis. Presumably phytoplankton with high photosynthetic rates are also in the process of converting photosynthetic products to new cellular material, and thus have a high rate of respiration. Phytoplankton with lower photosynthetic rates are not in an active growth phase, and therefore there is a closer relation between net and gross production. This relation between a net–gross production ratio and the growth phase of a population is not unique. Similar trends have been reported for the Sargasso Sea (Menzel and Ryther, 1959) and continental-shelf waters off the northeastern United States (Ryther and Yentsch, 1958).

The adjusted net and gross production values for the fjord are 455 and 609 g C/m²/yr, respectively. These are based on a summation of production values for both the nanno- and net-phytoplankton fractions of the incubated population sample. Comparisons of the fractions indicate that the nannoplankton were responsible for almost all fjord primary production during 1958–59. Only on two occasions, in February (90%) and in September (89%), was their contri-

TABLE V. Mean fjord gross primary production estimations adjusted for variations in insolation, corrected for respiration, and integrated to provide an estimate of the mean annual net and gross primary production of Indian Arm.

Date	Period	Total days	Mean fjord gross primary production (mg C/m³/day)	Mean daily insolation for period (langlies)	Mean daily insolation for *in-situ* incubations (langlies)	Light ratio	Corrected gross primary production (mg C/m³/day)	Mean fjord euphotic zone respiration (mg C/m³/day (24))	Corrected net primary production (mg C/m³/day (24))	Fjord net primary production (g C/m²/period)	Fjord gross primary production (g C/m²/period)
5–6 Nov.	29 Oct. 25 Nov.	26	483			assumed 1.00	483	250	233	6.1	12.6
16 Dec.	26 Nov. 26 Dec.	31	43			assumed 1.00	43	29	14	.4	1.3
6–7 Jan.	27 Dec. 30 Jan.	36	30			assumed 1.00	30	17	13	.5	1.1
24–25 Feb.	31 Jan. 13 Mar.	42	836	134.8	113.5	1.19	995	244	751	31.5	41.8
1–2 Apr.	14 Mar. 21 Apr.	39	1098	285.3	229.7	1.24	1362	488	874	34.1	53.1
12–14 May	22 Apr. 29 May	38	4610	405.0	397.0	1.02	4702	593	4109	156.1	178.7
16–18 June	30 May 3 July	34	3175	488.0	536.1	.91	2889	795	2094	71.2	98.2
21 July	4 July 18 Aug.	46	1108	508.5	596.8	.85	942	578	364	16.7	43.3
17–18 Sep.	19 Aug. 3 Oct.	46	2481	278.7	246.4	1.13	2804	731	2073	95.3	129.0
22 Oct.	4 Oct. 28 Oct.	25	670	150.2	50.0	3.00	2010	285	1725	43.1	50.3
								Annual total: (mg C/m²/year)		455.0	609.4

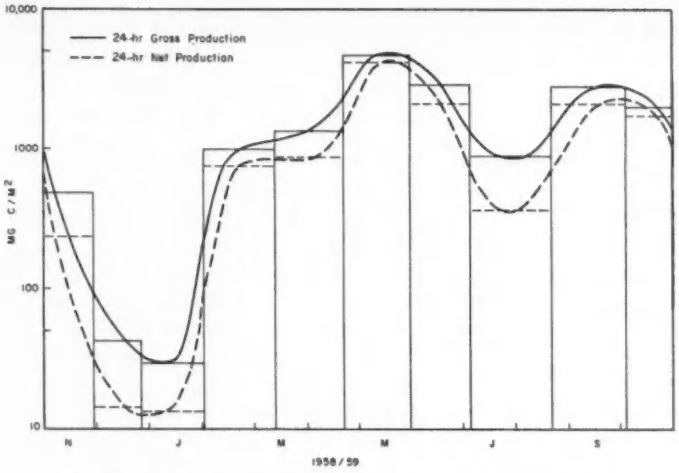

FIG. 8. Seasonal variation in gross and net primary production.

bution observed to fall below 92%; and during the period from May through July their average contribution was over 99%.

The period of time between observations makes it difficult to relate the changes in nannoplankton contribution to bloom development. However, it is suggestive that the series prior to the spring bloom shows a steadily decreasing contribution from the net phytoplankton; 10% in March, 5% in April, and 0.5% in May. The converse trend is present during the fall bloom. This suggests that the nannoplankton are relatively most important during the spring bloom and least important during the fall bloom, and is partially supported by standing crop measurements (Gilmartin, unpublished data) which show a marked peak in September of 1959.

5. ENVIRONMENTAL CONTROL OF PRIMARY PRODUCTION

The annual cycle of production in Indian Arm is established through the influence upon the photosynthetic population of environmental factors which influence its metabolism and affect its spatial distribution. These factors are not necessarily mutually exclusive, but their interaction and combination determine the production characteristics of the ecosystem.

5.1. FACTORS AFFECTING METABOLISM

The phytoplankton population of the fjord is in a state of flux as a result of the constantly changing oceanographic factors. With each new set of factors, the species best adapted to a particular environment develop and dominate the phytoplankton population. Under these conditions, factors which may influence the production rate of a particular species under laboratory conditions decrease in importance in the fjord ecosystem. As conditions become unfavourable for one species, another better-adapted one replaces it. In a broad sense, the

factors which can be expected to influence the production of the population are: the amount of available light, concentration of essential nutrients, and temperature.

a. LIGHT

The energy necessary for the photosynthetic production of organic material is provided by light. It is now known that some species can adapt to changing light intensities, particularly in raising the photosynthetic efficiency under conditions of low light intensity (Kok, 1951). The major groups of algae making up the phytoplankton have different light requirements (Strain, 1951). The concept of seasonal succession and adaptation of species under different conditions has been pointed out by Rodhe *et al.* (1958). Steemann Nielsen and Jensen (1957) conclude that in the sea as a whole (excluding the Arctic and Antarctic), light is not a major limiting factor in production. Sufficient light energy is usually available for the production that can occur with the nutrients available in the euphotic zone. However, physical movements of the water can carry the phytoplankton to depths lacking sufficient light for maximum production.

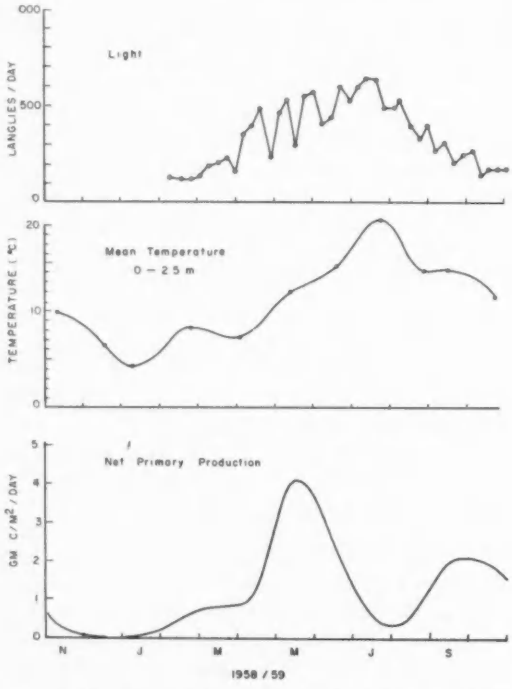

FIG. 9. Seasonal relation between total daily incident radiation, euphotic zone temperature, and net primary production.

The comparison of the annual production cycle in Indian Arm (Fig. 9 and Table V) with the seasonal availability of radiant energy points out the significance of the above conclusions. The year's gross production minimum occurred in December and January, with a daily production of 0.04 and 0.03 g C/m², respectively. By February the production rate had increased to 1.00 and it continued to increase until the spring maximum of 4.70 g C/m² was attained in May. This increase in production during the spring months was not associated with a marked increase in available radiant energy. Quite the contrary, the production increase preceded the radiant energy increase by approximately two months. At the time of the March upswing in production, the available radiant energy was not appreciably different from the preceding two months, which had the lowest production values of the year. This suggests that factors other than radiation affected both the time and magnitude of the midwinter low of production. This midwinter low is probably related to the maximum surface transport occurring at this time.

b. NUTRIENTS

The problem of the nutrient production relation is much more complex than was originally suggested by Brandt (1899), who hypothesized that phytoplankton production was dependent on the availability of only nitrates and phosphates. Subsequent work tended to support this concept. Consequently, because the ionic ratio in the sea is quite constant, there was a tendency to evaluate the effects of nutrients on phytoplankton growth by the consideration of one element alone. The ease of analysis for phosphate-phosphorus concentrations produced a large amount of data concerning the relation between phosphate and production, with the implication that such relation held for the other nutrients as well. However, Cooper (1937) showed that the ratio of nutrients departed significantly from the reported "normal" ratio, particularly in enclosed seas (and by analogy, in estuaries). This concept was supported by Riley and Conover (1956) in their studies in Long Island Sound, where they found nitrogen: phosphate ratios of 8:1, about half the 15:1 reported for the open sea (Sverdrup *et al.*, 1942). When the possible variation in primary nutrient ratio is considered, combined with the fact that silicate, iron, manganese (Harvey, 1957), organic growth factors (Provasoli and Pitner, 1953), and ectocrines (Lucas, 1949, 1955) can also be limiting, the difficulty of determining a relation between nutrient levels and production without a complete series of nutrient analyses is apparent. Lacking such analyses, an estimate can be gained by considering the effect on nutrient level of the various known physical processes.

In Indian Arm the nutrient level is established by a combination of biogenic processes (including bacterial regeneration and algal utilization), and various transport mechanisms. The surface brackish layer occupies a large portion of the euphotic zone. As shown in Fig. 10, some 90% of total production of the water column usually occurs at depths less than 5 m. The level of nutrients within this layer depends upon the amounts of the nutrients contributed by fresh water discharge and the amounts entrained with the underlying saline water. Since the Indian River appears to bring in few nutrients (Gilmartin, 1962),

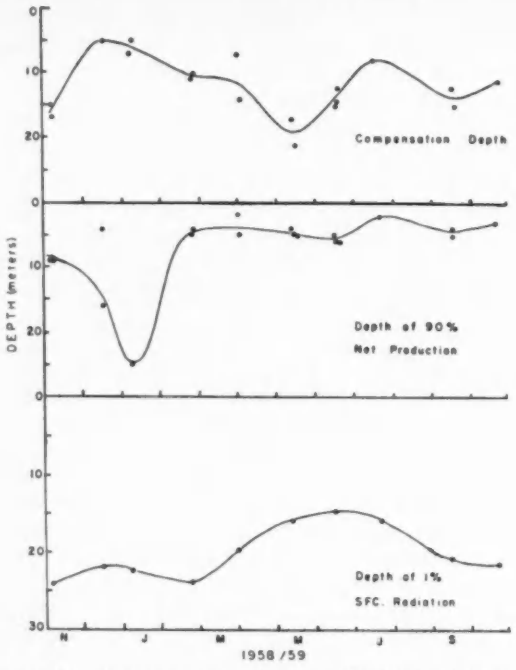

FIG. 10. Seasonal relation between the depth of compensation, the depth of 90% net primary production, and the depth of 1% surface radiation.

the level of nutrients in the euphotic zone results primarily from the concentration of nutrients in the underlying waters and the mechanisms which move them vertically.

The close correspondence between stability and production (Fig. 11) suggests that this factor plays an important role in establishing the type of production cycle in Indian Arm. Two mechanisms relate stability to production. High stability favours the maintenance of the phytoplankton population in a zone of favourable light intensity but restricts the vertical transfer of nutrients. Low stability favours the vertical replenishment of nutrients in the euphotic zone. However, it also allows the phytoplankton population to be moved vertically to less favourable mean-light intensities. Thus, the vertical movement of the phytoplankton may take them through regions of both favourable and unfavourable light conditions, and their production results from the *mean* light energy received. Prior to the initiation of each production peak, a period of low stability occurred, whereas, during each production peak the stability was increasing. This particular cycle of stability then can be visualized as actin in the following manner. The period of low stability permits a replenishment of nutrients in the euphotic zone, followed by a period of high stability favourable

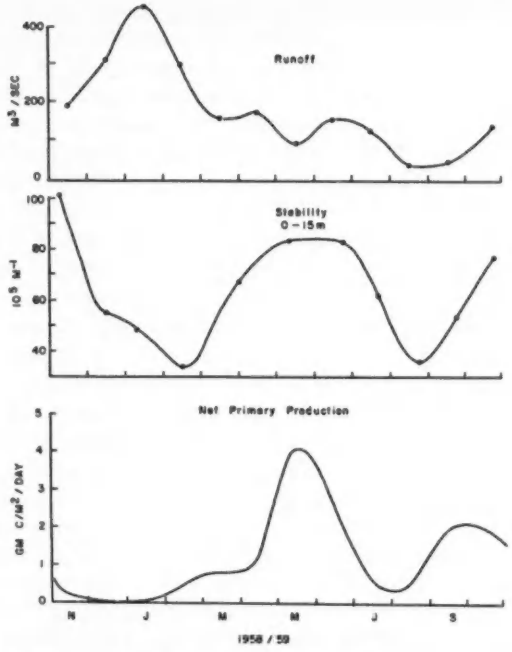

FIG. 11. Seasonal relation between runoff, water column stability and net primary production.

to the maintenance of production by the population at favourable depths. However, continued high stability results in the depletion of nutrients, which may then become limiting factors.

c. TEMPERATURE

A comparison of the annual cycles of temperature and production in Indian Arm (Fig. 9) shows little if any direct correlation between them. A possible exception occurs in July, when the maximum temperature coincides with the mid-summer production minimum. This general lack of correlation might be expected for two reasons. First, the phytoplankton population is in a constant state of flux as the species complex changes in adaptation to fluctuating environmental conditions. As a result, there is a strong tendency for species to exist under their optimal temperature requirements. In addition, great adaptation to changing temperatures is possible (Steemann Nielsen, 1955). Secondly, temperature would be expected to act metabolically, either through an effect on photosynthesis or on respiration. It has been reported that under conditions where light is not the limiting factor, there is little or no direct temperature effect on the photosynthesis of phytoplankton (Baly, 1935; Baker, 1935; Riley *et al.*, 1949). The same cannot be said for respiration. *A priori*, one expects the rate

of respiration to increase with temperature. If the same population were present under all temperature conditions, an increase in respiration would result in a low value of observed net primary production. However, qualitative studies of the Indian Arm phytoplankton (Gilmartin, unpublished data) show the customary seasonal succession of species. With such an ever-changing species composition, the direct effect of temperature on primary production is difficult to establish. In investigations conducted in Scandinavian fjords, no direct relation was noted between primary production and temperature (Steemann Nielsen, 1940, 1951). This conclusion is partially supported by my data from light and dark bottle determinations of photosynthesis and respiration in Indian Arm.

5.2. Factors Affecting Population Distribution

The horizontal and vertical circulation pattern of the fjord controls the recruitment, depletion, and distribution of the phytoplankton population. At times the fjord waters and their contained phytoplankton are completely replaced. One such replacement took place in the spring of 1957 (Gilmartin, 1962), and a similar flushing appears to have taken place in the spring of 1960 (Anon., 1960). During periods between flushing, the population is continually depleted by two mechanisms. First, during each tidal exchange, a portion of the population near the mouth is transported out of the fjord. Secondly, the continual surface outflow removes portions of the surface layer (0–10 m). This depth range includes the effective portion of the euphotic zone. The rate of such outward movement is associated with the annual cycle of freshwater discharge into the fjord. At times, for example during the 1959 spring maximum discharge, transport values in excess of 400 m^3/sec occurred. At this rate, a volume equal to the upper 10 m of the entire fjord water mass (and its contained phytoplankton) would be transported out of the fjord every 5 days. At the other extreme, during the 1959 summer minimum, the observed transport was 40 m^3/sec, a rate which would take 52 days to remove an equal volume of water.

This transport of water out of the fjord removes a portion of the photosynthetically effective population. However, it also brings about an increased entrainment from underlying waters. These vertical movements tend to replace with "seed stock" the phytoplankton removed from the euphotic zone of the fjord. The relative effectiveness of these two mechanisms is difficult to establish. It is noteworthy that a comparison of the seasonal pattern of the runoff with the seasonal distribution of production shows a nearly inverse relation (Fig. 11). The spring-production bloom begins at the same time that the spring runoff slackens, and the fall-production bloom diminishes at the beginning of the winter runoff.

The two chief inflow mechanisms of fjord circulation (tidal action and compensating inflow—Gilmartin, 1962) recruit phytoplankton, but on a smaller scale. During each tidal cycle a volume of water equal to the tidal lens of the fjord is intoduced. The extra fjord phytoplankton contained in this water may or may not join the effective phytoplankton population of the fjord. There is a strong tendency for the inflowing tidal water and compensating water to

move in at depths well below the euphotic zone. Under these circumstances, the recruited phytoplankton may not survive to add to the effective phytoplankton population. An exception occurs during late summer, when appreciable quantities of the inflowing waters move in at depths just below the surface brackish layer. These depths vary from 10 to 20 m. Phytoplankton introduced in this way is added to the effective phytoplankton population of the fjord.

6. DISCUSSION

A comparison of the annual production in Indian Arm with that of other estuarian habitats is difficult, because few data are available on the *annual* cycle of organic production in marine estuaries. Representative figures for a series of some estuarian and coastal habitats are presented in Table VI. Data from other, earlier work (e.g. Gaarder and Gran, 1927) are excluded because the long incubation periods used are difficult to interpret. Because annual production estimates are scarce, representative sets of daily production data are compared for certain coastal and estuarian habitats.

The estimated annual production of Indian Arm is higher than that reported for other high latitude estuaries. Long Island Sound, the most intensively investigated estuary (and one of the few where the annual production cycle was established in detail), is reported to have an annual gross production of 470 g C/m²/yr (Riley and Conover, 1956), a value about 35% less than that estimated for Indian Arm. This disparity may result from the presence of a reserve of nutrients in the deep water basin of the fjord, a feature lacking in other types of estuaries.

The radiocarbon and oxygen-budget methods used to estimate net and gross production in this study are complementary. The values calculated by the oxygen method provide three estimates: the amount of organic material produced in excess of the fjord requirements; the amount of organic material utilized by respiration in the sub-euphotic waters of the fjord; and the gross fjord production. The mean values for 1958–59 were 381, 290 and 671 g C/m²/yr, respectively. The C^{14} method is assumed to provide a measure of daylight net primary production. Adjustment of these values, using respiration data, provides an estimate of the 24-hr net and gross primary production. Further adjustment for variations in insolation provide annual production estimates comparable with those produced by the oxygen budget method. The mean fjord values for 1958–59 were 455 and 609 g C/m²/yr, respectively. Therefore, based on these two different methods, a production value of 600–675 g C/m²/yr is believed to be a realistic estimate for gross annual production. The estimated deep-water utilization of organic material was found to be 290 g C/m²/yr, and the net primary production 380–455 g C/m²/yr. The difference between these two values provides an estimate of the amount of organic material not utilized within the fjord. Since analysis of the bottom sediments indicates that very little organic material is deposited on the bottom, this difference also represents that amount of material transported out of the fjord. Assuming that 5% of the organic material produced is present as detritus undergoing decomposition in the fjord

TABLE VI. Selected examples of productivity measurements.

Locality	Time	g C/m²/yr	Mg C/m²/day	Method	Reference
Indian Arm		670		O_2 budget (gross)	author
Indian Arm		450		C^{14} (net)	author
Long Island Sound		470		O_2 and PO_4 budget (gross)	Riley and Conover, 1956
Isefjord		175		O_2 L-D incubation (gross)	Steemann Neilsen, 1951
Puget Sound		30–111		PO_4 budget	Waldichuck and Gould, MS, 1953
Trevor Channel		52–62		O_2 and PO_4 budget	Waldichuck, 1956
Georges Bank		309			Riley *et al.*, 1949
Gulf of Maine		270		PO_4 budget (gross)	Riley, 1941
Indian Arm			24–3700	C^{14} (net)	author
English Channel	June		500	C^{14} (net)	Steemann Neilsen, 1954
Ecuador coastal	Autumn		500–1000		Holmes *et al.*, 1957
S. W. Africa coastal	Autumn		500–4000	C^{14} (net)	Steemann Neilsen, 1954
N. Y. Coastal	April		250	Chlor. *a* and light (gross)	Ryther and Yentsch, 1958
Kattegat	Oct.		250	O_2 L-D incubation (gross)	Steemann Neilsen, 1937
	Dec.		10		
Danish coastal	Mar.		300	C^{14} (net)	Steemann Neilsen, 1958
	Aug.		700		
Florida (turtle grass bed)			4650	O_2 budget (gross)	Odum, 1957
Marshall Is. (coral reef)			3500	O_2 budget (gross)	Odum and Odum, 1955
Hawaiian Is. (coral reef)			2900	O_2 budget (gross)	Kohn and Helfritch, 1957

basin, these calculations indicate that about 25% of the fjord production is exported. This is consistent with the pattern of circulation, which has a constant net outflow of the shallow surface layer — a layer where most primary production occurs. A comparison of the utilization and production curves (Fig. 12) provides three interrelated cycles: an annual cycle of utilization, an annual cycle of net production, and an annual cycle of gross production. The comparison of these curves indicates that the material produced within the fjord during the spring and early summer tends to be used within the fjord whereas that produced during the fall tends to be exported.

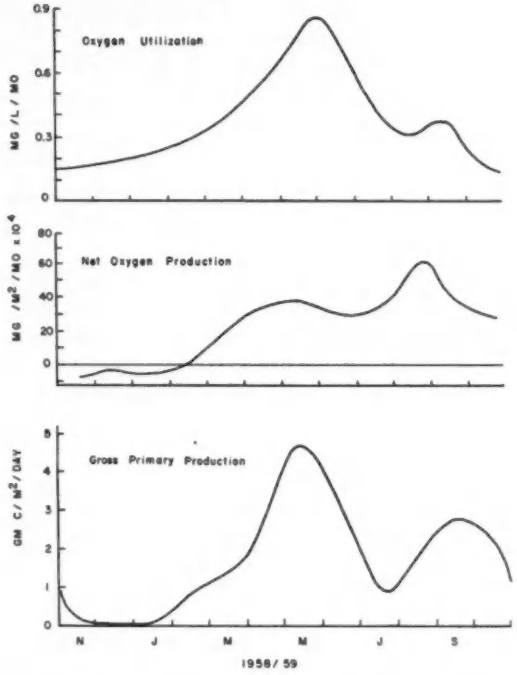

FIG. 12. Annual cycles of oxygen utilization, oxygen production, and gross primary production.

7. SUMMARY

1. From data gathered on 35 cruises at monthly intervals from 1956 through 1959, the distribution of conservative and non-conservative oceanographic properties in Indian Arm were determined. From an analysis of the cycles of distribution of these properties, as well as from direct current measurements, the circulation pattern and method of fjord water replacement were determined.

2. The annual cycle of primary production was established by analysing the changes in the quantity of dissolved oxygen within the fjord water mass by complementary methods: a net oxygen budget method — to determine the amount of organic material produced in excess of the fjord's requirements; an oxygen-utilization method to estimate the amount of oxygen utilized in sub-euphotic waters; and a gross production method — to estimate the total amount of organic material produced within the fjord. The values for 1958–59 were estimated to be 381, 290, and 671 g C/m²/yr, respectively.
3. The annual cycle of primary production was also established using the C^{14} technique with *in-situ* incubation. Subsequent correction of these data for observed respiration and variations in insolation, provided estimates for 1958–59 net primary production (24) and gross primary production of 436 and 609 g C/m²/yr, respectively.
4. The amount of gross primary production exported to neighboring waters was estimated to be approximately 25%.
5. The relative contributions of the nanno- and net-plankton fractions to primary productions were established, and it was shown that over the year more than 90% of the primary production is attributable to the nanno-plankton.
6. The relations between the physical environmental factors and primary production are discussed. The primary factor controlling productions is believed to be yearly variations in the stability of the water column. The variable stability influences the mean light intensity received by the phyto-plankton population, and effects the replenishment of nutrients in the euphotic zone.

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Polyphosphate Treatment of Frozen Cod. 2. Effect on Drip, Yield, Lipid Hydrolysis and Protein Extractability in Twice-Frozen Newfoundland Summer Trap and Fall Cod[1]

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ABSTRACT

Thaw-drip from once-frozen fall-caught Newfoundland cod (*Gadus morhua* L.), thawed after storage at −23°C for up to 13½ weeks, was equal to total drip from twice-frozen fish treated with sodium tripolyphosphate between freezings. Treatment of twice-frozen cod before the first freezing only had no effect on reducing total thaw-drip below that from twice-frozen untreated samples and the yield, although higher in the former than in the latter, was no better than that from once-frozen untreated fillets. Yields from twice-frozen fish were improved greatly by dipping prior to the second freezing and by dipping before each freezing. Treatment between freezings gave yields close to 100% of initial fillet weight whereas losses with the untreated once- and twice-frozen product appear close to 7 and 15%, respectively.

With summer-caught trap fish, characterized by higher thaw-drip values which were not affected by treatment, yields of twice-frozen cod were improved; however, losses were still about 12% in fish treated between freezings.

Treatment of twice-frozen cod from the two sources did not appreciably affect lipid hydrolysis or protein denaturation. However, lipid content and free fatty acid production were significantly higher in the trap fish samples as compared to the fall-caught cod.

INTRODUCTION

In recent years the Newfoundland fishing industry has shown interest in adding to the volume of fish used for the production of frozen blocks of finished groundfish fillets. Until now, the supply has been principally iced or un-iced fresh cod (*Gadus morhua* L.). Thus, rough-cut[2] fillets and eviscerated, unfilleted fish frozen at sea or at distant areas of the long coastline are among possibilities for increased supplies. In large-scale commercial operations involving two freezings, the use of sodium tripolyphosphate to improve moisture retention would undoubtedly be considered since fillets being used in well over one-third

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[2]Fillets of rough-cut or rough-filleted fish are those removed from either eviscerated or uneviscerated fish, and are not skinned, trimmed or boned.

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of the once-frozen commercial pack are currently being treated. It was considered worthwhile therefore to compare twice-frozen cod treated with sodium tripolyphosphate with cod from the same lot which had not been treated. In work carried out concurrently (Dyer *et al.*, 1964) on once-frozen cod fillets stored at −12°C (+10°F), tripolyphosphate treatment had little effect on lipid hydrolysis, protein extractability and thaw-drip, but a higher yield of frozen and of thawed product was obtained. In the present investigation, sodium tripolyphosphate used in amounts to increase the phosphate in the fillets by about 0.15 to 0.19% phosphorus at each application was used before the first freezing only, before the second freezing only, and before both freezings in samples of twice-frozen fall-caught Newfoundland shore cod. The development of thaw-drip, lipid hydrolysis and changes in protein solubility were studied. A single dip only, applied between first and second freezings, was tried on twice-frozen Newfoundland trap fish. Estimated yields of once- and twice-frozen samples are reported.

EXPERIMENTAL

1962 Fall-caught Fish

A quantity of gutted cod of 5-lb size, caught by trawl line at Catalina, Trinity Bay on October 23 was landed in about 3 hr without ice. The fish temperature was 6°C and they were in pre-rigor condition. Two fish were filleted and skinned immediately and the finished fillets, packed in 1-lb waxed paper cartons and plate frozen in 1–1¼ hr, were stored as controls at −23°C (−10°F) in a commercial cardboard master carton. The remaining fish were filleted but were not skinned, trimmed or boned. Of these, 26 lb were dipped in a 9% solution of sodium tripolyphosphate for 2 min; the ratio of weight of fish to weight of dip was 14:1 (Mahon, 1962). The treated fillets and a remaining undipped lot of 17 lb were plate frozen in about 2 hr in separate 2¼-inch-thick waxed paper enclosed blocks and stored at −23°C. Two weeks later the treated and untreated rough fillets were thawed dielectrically, and then skinned, boned and trimmed. The dielectric process has been described in general by Jason and Sanders (1959, 1962a, b). The blocks were raised from an average temperature of −18°C to about 0°C after 95 min exposure to radio frequency energy. Fillets from each lot were divided into two portions, one portion of which remained untreated while the other was dipped in sodium tripolyphosphate as before. The four lots of finished fillets were packed in 1-lb packages and plate frozen in 1–1¼ hr. All samples were transported to St. John's in insulated, dry-ice-refrigerated containers. Half of each of the four lots of twice-frozen finished fillets were stored at −23°C (−10°F) and half at −12°C (+10°F) in commercial cardboard master cartons. The once-frozen control was stored at −23°C. Once- and twice-frozen samples were examined after 0, 5½, 13½ and 20 weeks refrozen storage.

1962 Trap Fish

In July, a quantity of 3- to 4-lb trap fish was boated off Catalina, Trinity Bay, iced, landed and eviscerated, re-iced and held for 24 hr. They were then headed and washed and half were frozen in blocks (not filleted and still in rigor)

in 4-inch-deep waxed paper cartons in about 5½ hr in a horizontal plate freezer. The waxed cartons were then wrapped in 4-mil-thick (.004-inch) polyethylene sheets, sealed with masking tape and stored at −23°C. The other portion was immediately filleted and plate frozen in 1-lb packages of finished fillets as described above. These samples were stored in commercial cardboard master cartons at −23°C. After 3 months, the blocks of unfilleted fish were thawed dielectrically. The fish were in the thawer for 1 hr after which the samples were "tempered" in ice for 1 hr. The fish were then filleted, skinned, boned, and trimmed, and divided into two equal portions. One portion of the fillets was left as a control and the second treated with tripolyphosphate as above. Both were packaged in 1-lb cartons, plate-frozen in 1–1¼ hr and packed in commercial cardboard master cartons. All samples were transported to St. John's and stored as described for the fall fish samples.

Laboratory Determinations

Thaw drip was determined by a procedure similar to that used by Hartshorne and Puncochar (1951). Samples of 50–100 gm of frozen fillet were placed in a stainless steel sieve, which in turn was placed in a funnel over a graduated cylinder. The whole apparatus was enclosed in a tight-fitting polyethylene bag to prevent evaporation and left to thaw in a cold room at 2–3°C (35–37°F) for 48 hr as described by Dyer *et al.* (1962).

Frozen samples were analyzed for extractable protein (EPN) by the method of Dyer *et al.* (1950, 1964).

Total lipid was extracted by the chloroform–methanol phase separation procedure (Bligh and Dyer, 1959). Free fatty acids (FFA) were titrated against alcoholic NaOH. Results were calculated for a fatty acid average molecular weight of 300.

Total phosphate was determined by the volumetric method (Anon., 1960) using concentrated nitric acid for digestion. Results are reported as percentage total phosphorus.

The average of duplicate determinations are reported for FFA, extractable protein, and phosphorus.

RESULTS AND DISCUSSION

Phosphorus Uptake

1962 fall-caught fish

Total phosphorus in the untreated controls of the once- or twice-frozen fall fish average 0.20% (Table I), in agreement with previously reported values in cod flesh (Dyer *et al.*, 1958). Phosphorus uptake in the fall fish treated once with sodium tripolyphosphate before the first or second freezing amounted to 0.16 and 0.19% P, respectively, and 0.32% for the samples treated prior to each freezing. Expressed as sodium tripolyphosphate (25% P), this represents uptakes of 0.64, 0.76 and 1.28%, respectively. This uptake agrees with the value of 0.64% calculated on the assumption that all the dip is absorbed and is distributed uniformly through the flesh.

TABLE I. Extractable protein, total lipid, free fatty acids and thaw-drip in sodium tripolyphosphate-treated twice-frozen fillets of Newfoundland fall cod stored at −23 and −12°C.

	Storage temperature						
	−23°C				−12°C		
	Time in weeks				Time in weeks		
Sample[a] and analysis	0	5½	13½	20	5½	13½	20
Phosphorus (% wet wt)							
(1)	–	–	0.21	0.19	–	–	–
(2)	–	–	0.20	–	–	0.19	0.23
(3)	–	–	0.42	0.31	–	0.40	0.30
(4)	–	–	0.37	0.40	–	0.35	0.43
(5)	–	–	0.51	0.54	–	0.49	0.56
Drip (% wet wt)							
(1)	7.0	10.5	4.4	(7.9)	–	–	–
(2)	10.2	13.0	10.9	(6.5)	11.6	(2.6)	(1.1)
(3)	11.6	13.9	14.3	(7.1)	13.7	(11.0)	(2.4)
(4)	2.3	3.3	6.7	(5.2)	2.9	(6.2)	(5.8)
(5)	5.6	11.4	9.9	(7.1)	9.2	(10.2)	(7.3)
Total lipid (% wet wt)							
(1)	0.64	0.67	0.71	0.65	–	–	–
(2)	0.58	0.79	0.62	0.77	0.68	0.73	0.55
(3)	0.55	0.68	0.69	0.65	0.64	0.67	0.63
(4)	0.38	0.65	0.62	0.70	0.64	0.55	0.47
(5)	0.44	0.65	0.66	0.80	0.52	0.58	0.50
FFA (% total lipid)							
(1)	11.6	19.7	20.3	26.2	–	–	–
(2)	10.5	16.3	19.4	25.1	48.0	52.2	52.4
(3)	12.2	16.6	19.9	23.4	42.0	51.9	49.8
(4)	13.6	16.6	19.3	21.4	32.6	49.9	62.4
(5)	12.8	11.7	19.4	21.4	34.6	47.3	51.7
Protein (% wet wt)							
(1)	–	–	–	2.28	–	–	–
(2)	–	–	–	–	–	–	0.63
(3)	–	–	–	2.08	–	–	0.51
(4)	–	–	–	2.12	–	–	0.66
(5)	–	–	–	1.69	–	–	0.60

[a]Sample treatment: (1) once-frozen, undipped controls; (2) twice-frozen, undipped controls; (3) twice-frozen, dipped prior to first freezing; (4) twice-frozen, dipped prior to second freezing; (5) twice-frozen, dipped prior to both freezings.

1962 TRAP FISH

Untreated once- and twice-frozen samples contained about 0.2% P (Table III). Added phosphate in fillets dipped before the second freezing amounted to about 0.15% P.

THAW DRIP

Since the samples had not been overwrapped, dehydration became evident at the 12 and 13½ weeks sampling at −12°C and at the 20 and 22 weeks sampling at −23°C. Free drip values were reduced and are recorded in parentheses because of their somewhat dubious value. They do indicate that thaw-drip may be reduced under such conditions. Moisture content was not determined, but the high protein extractability in the 20-week sample at −23°C indicates that drying was not sufficient to appreciably affect extractability of the actomysin even though the latter is very sensitive to dehydration (Dyer *et al.*, 1950). Presumably also there may have been some effect on lipid hydrolysis at the longer storage times.

1962 FALL-CAUGHT FISH

For the five treatments the averages of drip values (Table I) up to and including 13½ weeks refrozen storage at −23°C are 7.3, 11.4, 13.3, 4.1 and 9.0% wet weight, respectively. Table II shows data on thaw-drip from the electronically-thawed blocks from which the twice-frozen samples were prepared (MacCallum, 1964). The latter losses added to those in Table I represent total thaw-drip (Table II).

Total drip losses for the two thaws ((a) the dielectric thaw of blocks of rough fillets and (b) the slow laboratory thaw of the small portions of processed, refrozen fillets) were substantially less when samples were dipped before the second freezing, than in the case of dipping prior to the first freezing or when samples were not treated. Based on 7% weight uptake per dip, respective yields for the three cases under consideration would be: about equal to starting material (and about 7% better than that from the once-frozen untreated control); about 8% reduction from starting material (and about the same yield as that from the once-frozen untreated control); about 15% reduction from starting material.

TABLE II. Total thaw-drip and estimated yields from Newfoundland fall cod stored at −23°C.

Sample[a] and treatment	Maximum thaw-drip at time of dielectric thawing (between freezings)[b]	Total thaw drip after refrozen storage (time in weeks)			Estimated effect of treatment on yield from starting material
		0	5½	13½	
(1)	–	7.0	10.5	4.4	−7%
(2)	3.3	13.5	16.3	14.2	−15%
(3)	1.9	13.5	15.8	16.2	−8%
(4)	3.3	5.6	6.6	10.0	No change
(5)	1.9	7.5	13.3	11.8	+3%

[a]See Sample treatment (footnote, Table I).
[b]See MacCallum (1964).

It is recognized that losses from the electronically-thawed blocks may have been small in relation to those from the small samples thawed in the laboratory because of the relative surface area to weight ratios in the two instances (MacCallum, 1964). In the former instance the ratio was about 1.2 and in the latter about 3.4. Notwithstanding, blocks prepared for dielectric thawing under commercial conditions will enjoy the advantage of low ratios of surface area to weight, possibly as low as 0.85 (for 14 × 42 × 3-inch blocks). Since the results are only approximate estimates and the electronic thawing loss was small, it was not considered worthwhile to apply corrections for the difference caused by expressing thaw-drip values on the actual sample weight rather than converting to the original fish weight. The same argument applies to takeup of solutions in the dipped samples and analytical values will also be slightly affected.

Two dips resulted in no improvement in thaw-drip over a single dip before the second freezing. However, the yield from twice-dipped fish could still be higher because of two immersions.

With untreated fish, two freezings appeared to double thaw-drip losses over one freezing and estimated yields dropped approximately equal amounts with each freezing; that is, freeze-thaw and refreezing unquestionably decreased the yield.

1962 TRAP FISH

Results (Table III) are reported for thaw-drip from *finished* fillets only. Drip values are considerably higher than for fall-caught samples. Thaw-drip from once-frozen untreated trap fish fillet controls was consistently lower than that from the refrozen fillets, averaging about 12.5% as compared with about 18% for the refrozen fillets. There was little difference in amounts of thaw-drip from *finished* fillets in the case of twice-frozen samples dipped before the second freezing and from those not dipped at all. The losses at first thawing, as determined for fall-caught fish, are not available. Even if initial losses had been low, total losses would be quite high, much more than with fall-caught samples. Overall yields from once-dipped, twice-frozen samples would not be good and would show a drop of at least 12% from the starting material. Yields from undipped twice-frozen samples were even less, showing a drop of at least 19% from starting material. The yield from once-frozen untreated controls dropped at least 13% from starting material.

GENERAL

Total drip values (Table II) which averaged 14.7% for the refrozen fall fish are higher than those reported by Hartshorne and Puncochar (1951) on round frozen cod, which averaged 1.4 and 1.8% for samples frozen on catching and after icing for 10 days prior to freezing. The round fish were held 10 days prior to thawing and refreezing. Values for haddock averaged 1.3%. On the other hand, when the frozen round fish were stored 10 weeks prior to thawing and refreezing (haddock only) drip values on the refrozen fillets stored at −10°C were more than doubled, 2.3 to 5.2%.

TABLE III. Extractable protein, total lipid, free fatty acids and thaw-drip in sodium tripolyphosphate-treated twice-frozen fillets of Newfoundland trap cod stored at −23 and −12°C.

	Storage temperature						
	−23°C				−12°C		
	Time in weeks				Time in weeks		
Sample[a] and analysis	0	7	12	22	7	12	22
Phosphorus (% wet wt)							
(1)	–	–	–	0.21	–	–	–
(2)	–	–	0.17	0.23	–	0.14	0.22
(3)	–	–	0.31	0.33	–	0.37	0.35
Drip (% wet wt)							
(1)	7.7	14.4	15.4	(10.4)	–	–	–
(2)	19.8	19.4	16.4	(16.5)	13.3	(3.8)	(6.5)
(3)	17.2	16.2	19.9	(8.9)	12.5	(4.6)	(0.6)
Total lipid (% wet wt)							
(1)	0.92	0.95	0.92	0.95	–	–	–
(2)	0.92	0.96	0.98	0.92	0.92	0.90	0.68
(3)	0.93	0.89	0.97	0.87	0.84	0.98	0.86
FFA (% total lipid)							
(1)	16.9	16.4	21.2	20.2	–	–	–
(2)	17.9	19.2	23.8	32.0	31.2	45.4	75.2
(3)	18.9	24.2	19.7	27.4	42.6	43.3	47.3
Protein (% wet wt)							
(1)	–	–	–	2.09	–	–	–
(2)	–	–	–	1.74	–	–	0.70
(3)	–	–	–	1.89	–	–	0.50

[a]Sample treatment: (1) once-frozen, undipped controls; (2) twice-frozen, undipped controls; (3) twice-frozen, dipped prior to second freezing.

In the previous paper (Dyer *et al.*, 1964) drip values for once-frozen offshore cod fillets range from 4.3 to 13%, almost identical to the present values for fall-caught cod, 4.4 to 10.5%. The higher values for the trap cod fillets, 7.7 to 15.4% for once-frozen, and 16.4 to 19.8% for the twice-frozen agree with previous results on Newfoundland trap fish (Dyer *et al.*, 1962).

With once-frozen fillets, polyphosphate treatment had little effect on drip (Dyer *et al.*, 1964)[3], and in the present work with fall-caught fish dipping prior to the first freezing resulted in about the same thaw-drip in the product as in the twice-frozen control fillets (Table I). However, dipping prior to the second

[3]*Note added in proof:* Subsequent work, now being prepared for publication, has shown significant drip reduction and reduced toughness in stored fillets of trap cod treated with sodium tripolyphosphate as compared with untreated controls.

freezing only, reduced product thaw-drip considerably. Thus polyphosphate treatment may reduce drip in some instances. For the producer, however, the greatly increased yield of both frozen and of thawed product where polyphosphate is used is of paramount interest. Yields from fall fish are close to 100% of the starting material, whereas losses with the twice-frozen, untreated product are approximately 15%.

FFA Development

1962 fall-caught fish

Treatment with sodium tripolyphosphate had no effect on FFA development (Table I) which proceeded at the same rate in once- and twice-frozen fillets. Both once-frozen control fillets and twice-frozen treated and untreated fish stored at −23°C started off with an initial value of about 12% of the total lipid present. For all samples and treatments, values had about doubled after 20 weeks. The total fatty acids formed was much the same in once- or twice-frozen or in polyphosphate-dipped samples (Fig. 1) with a major part of the increase occurring prior to 5 weeks storage, followed by a slower formation to 20 weeks storage.

At −12°C, on the other hand, FFA formation is only about one-half as rapid in the twice-treated and in the sample treated prior to the second freezing, as in the twice-frozen control. Maximum formation occurs at about 3 months, and values decline to approximately the 1-month level after 20 weeks storage. These levels and rates average very closely to samples 1, 2 and 3 of the previous paper (Dyer *et al.*, 1964).

1962 trap fish

At −23°C, the FFA increases very little in 22 weeks in the once-frozen control (Table III). Rates of formation of FFA at −23 and −12°C, when expressed as per cent of the total lipid, are very similar to the fall-fish values, although the initial level is higher as noted previously with trap fish (Dyer *et al.*, 1962). However, the average total lipid is very much higher in the trap fish (0.91 ± 0.014 for 18 samples) than in the fall fish (0.63 ± 0.10 for 32 samples). Thus, when the total amounts of fatty acids formed are considered (Fig. 1), that present initially in the refrozen fish is almost three times as much in the trap fish (average 166 mg/100 g muscle) as in the fall fish (average 62 mg/100 g). The amount formed on subsequent storage at either −23 or −12°C is about equal in both types of fish. Lipid hydrolysis at −23°C is quite slow in the trap fish and greater in the twice-frozen sample, whether treated with polyphosphate or not, than in the once-frozen sample. Thus polyphosphate treatment has not appreciably affected lipid hydrolysis. In the trap fish, the amount of lipid hydrolyzed is similar to that observed in the 1961 samples of refrozen trap fish, resulting in formation of much larger quantities of FFA than in the fall fish. The rate indicated is much higher than found for cod fillets by Dyer and Fraser (1959) or by Olley *et al.* (1962) and indicates enhanced enzymic activity in the trap fish fillets.

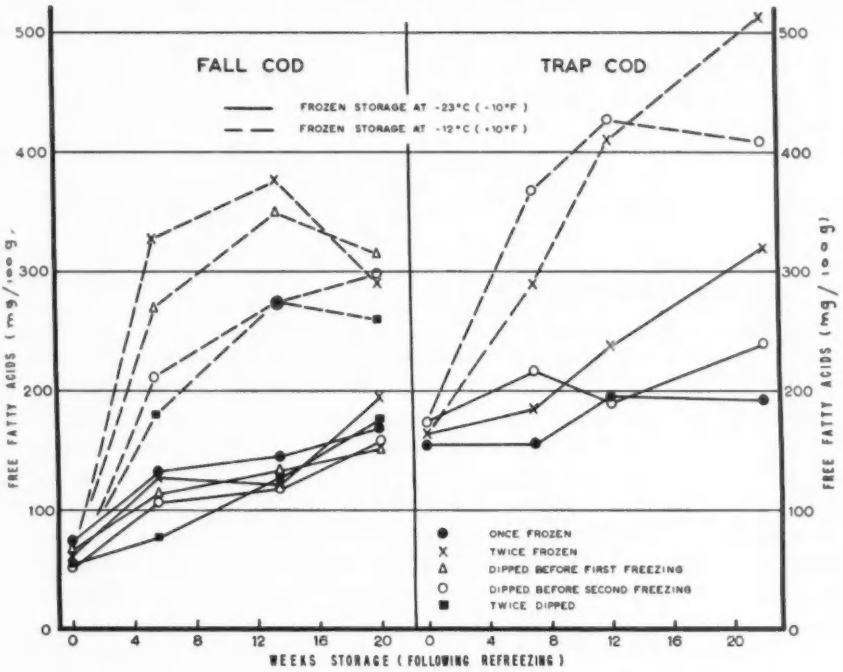

FIG. 1. Total free fatty acids formed in polyphosphate-dipped and in undipped twice-frozen cod fillets, and in undipped once-frozen controls held at −12 and −23°C.

EXTRACTABILITY OF SOLUBLE PROTEINS

FALL-CAUGHT FISH

After 20 weeks storage at −23°C, protein extractability by salt solution in the fall-caught fish (Table I) shows no decrease in once-frozen samples from that expected for freshly-frozen cod (Dyer and Dingle, 1961) but EPN values of the double-treated sample are somewhat low.

At −12°C, the EPN level of all samples is reduced by comparison with −23°C as would be expected.

1962 TRAP COD

Results (Table III) after 22 weeks storage show little effect from use of polyphosphate. Twice-frozen fillets at −23°C had somewhat reduced soluble fractions. The trap samples in general were poorer than the fall fish in this respect.

At −12°C, results were similar to those for fall samples stored at the same temperature.

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Incidence of *Ligula intestinalis* in Heming Lake Fish[1]

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ABSTRACT

Ligula intestinalis is found in a few species of Heming Lake fish, but occurs principally in the spottail shiner, *Notropis hudsonius*. A list of possible adult hosts is given. The largest *Ligula*, 91.4 cm long, was found in a sucker 29.5 cm long. Annual and regional differences in the incidence of *Ligula* in spottail shiners are noted. It is apparent that at Heming Lake, as in other regions, a large population of aquatic birds is not required to produce a high incidence of *Ligula* in fish.

INTRODUCTION

Ligula intestinalis Linnaeus, although a common parasite in the body cavity of several freshwater fishes, has not been ranked as a really important parasite by North American investigators. Its life history is reported by Dogiel *et al.* (1961), but details of the adult stage are not well defined. Dence (1958) summarized much of the previous work on *Ligula* in North America, describing its incidence in fish of Wolf Lake, near Newcomb, N.Y., U.S.A. He noted that larval *Ligula* were found almost exclusively in common shiners, *Notropis hudsonius*, that the gonads of infected fish were undeveloped, and that evidence indicated the American mergansers and great blue herons were the most likely definitive hosts.

Russian parasitologists have carried out extensive investigations, especially in reservoirs, on the occurrence of *Ligula* and, according to Dogiel (1957), *Ligula* is one of the frequent causes of mass disease of cyprinid fishes in native waters. According to Bauer and Stolyarov (1961), Kosheva in 1957 stated "Ligulosis in this reservoir is a serious disease at the present time, causing considerable losses to the fisheries," and "mortality of *Abramis brama* caused by *Ligula* was observed in many instances." According to Dogiel (1957), ligulosis is characterized by marked fluctuations from year to year and the incidence of *Ligula* was associated with the abundance of swimming birds as early as 1891. It is also reported in Dogiel (1957) that in some lakes temperatures appear unfavorable to ligulosis, and that high summer temperatures favor the development of ligulids. According to Bauer (1961), *Ligula*, parasitic in the visceral cavity of various cyprinids, suppresses the development of the ovaries of the host. Dogiel (1957) concludes that a wide distribution of ligulosis is associated with the presence of fish-eating birds in the body of water; however, to start a serious epidemic, it is not necessary to have a large population of birds on the body of water. The wide distribution of ligulosis in reservoirs is attributed to a large population

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of plankton, of which the copepod portion is a carrier of an intermediate stage of *Ligula*.

Some observations on the incidence of *Ligula* in fish of Heming Lake, Manitoba, have been recorded annually since 1958. It is hoped this information will add to a broader understanding of this cestode, particularly on this continent.

METHODS

The observations recorded in this paper were not part of a study designed to study parasites, but represent casual records made during the course of a fishing experiment. All fish that were captured and killed (from which data such as scales, sex, etc. were collected) were examined for parasites and identifiable species recorded. Since 1958, an attempt has been made to obtain a sample of spottail shiners to determine the annual incidence of infection. When the sample was unusually large, the length of host and length of parasite was recorded from a subsample of approximately 100 fish. The presence or absence of the parasite was noted for the balance of the sample.

RESULTS

Second Intermediate Hosts of *Ligula intestinalis*

In Heming Lake the most common host of *Ligula intestinalis* is the spottail shiner. The presence of the parasite in the body cavity of this shiner is easily noted, even without opening the animal, because the size of the parasite, in relation to the size of the host, causes a marked distention of the abdomen. Usually only one parasite is found in each infected shiner, but occasionally two may be found in the same host.

The white sucker, *Catostomus commersoni*, frequently carries the parasite, where it usually occurs in the coiled intestine. In most instances one parasite per sucker is common, but as many as five per host have been found.

The yellow perch, *Perca flavescens*, does not appear to be a major host of *Ligula* in this lake; however, the parasite has been recorded from several perch over the period of examination.

Possible Adult Hosts of *Ligula intestinalis*

The life history of *Ligula intestinalis* is dependent on the presence of fish-eating birds. Heming Lake does not support a large population of fish-eating birds, but, as mentioned earlier, a large number of birds is not required to cause a serious outbreak of the disease. Two or three pairs of common loons, *Gavia immer*, nest annually on Heming Lake and during mid or late summer as many as 12 to 24 loons (mostly juveniles) have been observed swimming together. Mergansers, *Mergus merganser*, are known to breed near streams flowing into the lake, but never more than two breeding pair have been observed during the summer. Herring gulls, *Larus argentatus*, are prevalent in the spring and early summer and are usually concentrated near a shore that served as the dumping ground for fish offal. Terns, *Sterna* sp., are fairly frequent visitors, but could be considered a transient rather than a resident population. Kingfishers, *Megaceryle alcyon*, are present around the lake in relatively low numbers.

Incidence of Infection in Major Second Intermediate Hosts

Notropis hudsonius, spottail shiner

In 1958, 12.5% of a small sample of shiners from a shallow productive region of the lake was infected (Table I). In 1959, 69% of a sample of 16 shiners from a creek flowing into Heming Lake contained *Ligula* (Table I). This creek is frequented by both loons and mergansers. A pair of mergansers breeds annually near this creek, and the close proximity of this possible adult host and the intermediate host may account for the high incidence of infection.

Table I. Incidence of *Ligula intestinalis* in spottail shiner, *Notropis hudsonius*. Numbers examined are shown in parentheses.

Length of fish examined (*mm*)	Year of sampling					
	1958	1959	1960	1963		
				A[a]	A	B[b]
40–49	0	No lengths	0 (0)	0 (1)	No lengths	No lengths
50–59	0 (1)	"	2 (13)	3 (10)	"	"
60–69	2 (6)	"	15 (55)	10 (49)	"	"
70–79	0 (5)	"	5 (21)	13 (32)	"	"
80–89	0 (4)	"	3 (10)	1 (10)	"	"
90–99	0	"	1 (1)	0 (3)	"	"
Total number infected:	2	11	26	27	340	179
Total number examined:	16	16	100	105	1047	332
Percentage infected:	12.5	69.0	26.0	26.0	32.5	54.0

[a]Both samples from same region on same day.
[b]Sample from different area.

In the area just offshore from the dumping ground for fish offal, 26% of a sample of 100 shiners contained *Ligula* in 1960 (Table I). The majority of the fish were between 50 and 80 mm in length. A comparable sample (both in size and in number of fish) in July 1963 had exactly the same degree of infection as in 1960. A larger sample, 1047 fish, from the same location and on the same day but for which no lengths were recorded, had a slightly higher level of infection (32.4%). There appear to be local differences in the rate of infection, as 54% of a sample of 332 shiners, from another area of the lake about one mile distant, captured at the same time in July 1963 carried *Ligula*.

Catostomus commersoni, white sucker

The suckers which have been examined for *Ligula* are fish removed from the lake either by experimental gill nets or are fish which for one of several reasons, such as loss of identifying tag mark, could not be returned to the lake. The incidence of *Ligula* is somewhat lower in suckers than in shiners, as seen on examination of Table II.

TABLE II. Incidence of *Ligula intestinalis* in common sucker, *Catostomus commersoni*. Numbers examined are shown in parentheses.

Length of fish examined (*mm*)	Year of sampling		
	1960	1962	1963
under 140	0 (119)	2 (2)	0 (1)
140–159	5 (2065)	1 (11)	2 (24)
160–179	14 (4409)	3 (28)	3 (56)
180–199	10 (3344)	0 (13)	0 (24)
200–219	6 (2194)	3 (12)	0 (14)
220–239	8 (1506)	5 (14)	0 (11)
240–259	7 (1306)	7 (7)	0 (14)
260–279	2 (707)	7 (40)	0 (24)
280–299	1 (387)	6 (75)	2 (70)
300–319	1 (207)	6 (41)	2 (75)
320–339	0 (275)	0 (126)	4 (120)
Total number infected:	54	40	14
Total number examined:	16,519	369	433
Percentage infection:	0.3	10.8	3.2

RELATIONSHIP OF LENGTH OF *LIGULA* TO LENGTH OF HOST

The relationship of length of *Ligula* to length of spottail shiner was not determined. The relationship of length of parasite to length of sucker is shown in Fig. 1. The wide scattering of points on the graph indicates very little association.

The longest parasite observed was 91.4 cm and was found in a 29.5-cm sucker; in fact, two 91.4-cm *Ligula* were taken from this small fish. It was not unusual to find parasites three times as long as their hosts. An 18-cm yellow perch contained a 62-cm *Ligula*.

DISCUSSION

The spottail shiner is a fairly important forage fish in the ecology of Heming Lake fish. It is evident from the data collected that this fish is the major host for *Ligula intestinalis* in Heming Lake. It has been demonstrated that *Ligula* is one of the frequent causes of mass disease among cyprinid fishes (Dogiel, 1957), and that marked fluctuations in the population size of *Ligula* from year to year is common. Our data show that not only are there annual fluctuations in inci-

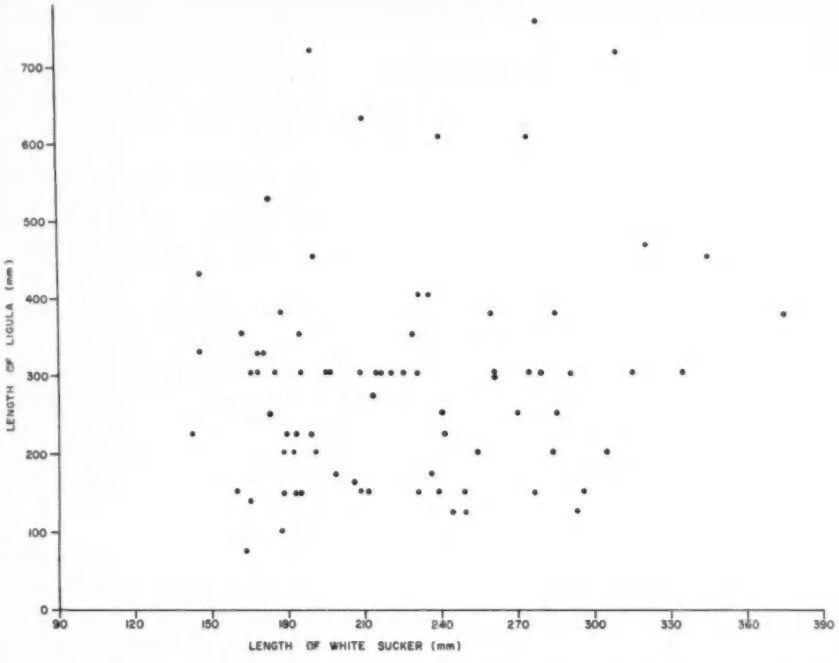

FIG. 1. Relationship between length of the intermediate host, white sucker (*Catostomus commersoni*) and length of parasite, *Ligula intestinalis*.

dence of *Ligula*, but also that there are marked regional differences. This latter fact is particularly striking when the 1963 samples are examined. The more heavily infected sample was drawn from an area of the lake which is highly productive, both in yield of fish and plankton. In some areas a high incidence of *Ligula* could be associated with habitat, as the possible adult host and the various intermediate hosts were in close contact. Data have not been collected over a long enough period to test the hypothesis that high temperatures are associated with high incidence of *Ligula*. Our results are certainly in close agreement with those that indicate a large population of aquatic birds is not required to produce a high incidence of *Ligula* in fish. The present study at Heming Lake consists mainly of tagging, marking and releasing fish and recapturing them to assess various population parameters in the hope of testing the validity of mathematical models used by fishery scientists to predict fishery yields under various conditions. None of the small fish, such as the spottail shiner, have been marked to date, but before long some effort will be directed towards an analysis of the fish biomass and an understanding of the possible mortality effect of parasites such as *Ligula*.

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Marine Ostracods from the Plankton of Indian Arm, British Columbia, Including a Diminutive Subspecies Resembling *Conchoecia alata major* Rudjakov[1,2]

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ABSTRACT

Four species of ostracods from Indian Arm, British Columbia, are characterized. *Paradoxostoma striungulum* Smith and *Conchoecia elegans* Sars, have variations not previously described. *Philomedes* sp., closely related to *P. carcharodonta* Smith, was represented by only one specimen. The fourth ostracod is one-third smaller than specimens of similar description which were obtained from the Pacific Ocean Weather Station "P" and which resemble most closely *C. alata major* Rudjakov. This smaller ostracod is proposed as a new subspecies, *C. alata minor*.

INTRODUCTION

The planktonic marine ostracods — cypridinids, halocyprids, and polycopids — were studied by Skogsberg (1920) who emphasized the taxonomic significance of details in the structure of the appendages. Recently Skogsberg's work has been supplemented by Iles (1961) who investigated the interrelation and function of the appendages in halocyprids.

Benson (1959) listed previous studies on Recent Ostracoda of the Pacific coast of North America. Smith (1952) recorded some Halocyridae from the Vancouver Island region of the Pacific coast. Rudjakov (1962) described three new species and two new subspecies of halocyrids from the northwestern Pacific.

In 1960 a study on the planktonic ostracods was carried out in Indian Arm, a coastal inlet of British Columbia, Canada. Four ostracods were collected: *Paradoxostoma striungulum* Smith, *Philomedes* sp., *Conchoecia elegans* Sars and a new subspecies, *C. alata minor*[4]. Collections examined for specimens of these ostracods were from other British Columbia inlets — Bute, Knight, Alberni, Tofino, Herbert, and Muchalat — and from the Pacific Ocean Weather Station "P". (Specific locations are given in later sections dealing with individual species.)

The four ostracods collected show some deviation from previous descriptions. The new subspecies is identical to specimens obtained from Station "P" except for being one-third smaller. The specimens from Station "P" resemble the description of *Conchoecia alata major* Rudjakov (Rudjakov, 1962).

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[2]From a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science in the Department of Zoology, University of British Columbia.
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[4]Repository for *Conchoecia alata minor*: British Museum (Natural History), registered number 1964-2-14-2.

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METHODS

Material from Indian Arm was collected using Clarke-Bumpus plankton samplers towed horizontally between the surface and the bottom, generally at vertical intervals of 30 m down to a maximum of 180 m. Specimens from the other British Columbia inlets were taken with an open, 1-m net, hauled from the bottom to the surface. The Station "P" material came from a single haul made between 1280 m and the surface.

For observation, whole specimens were held within glass depressions or mounted in glycerine jelly. Dissected specimens were stained with a combination of methylene blue and lignin pink and mounted in polyvinyl lactophenol (Salmon, 1949). Figures 3 and 16 were drawn freehand; others were drawn with the aid of a microprojector or a camera-lucida.

Unless otherwise stated the classification and terminology presented follow that proposed by Skogsberg (1920).

Order OSTRACODA
Suborder CYPRIFORMES
Family CYTHERIDAE
Subfamily PARADOXOSTOMINAE
Genus *Paradoxostoma* Fisher

Paradoxostoma striungulum Smith

Paradoxostoma striungulum Smith, 1952

OCCURRENCE

In the present study, the only specimens collected were from 0, 20, and 25 m in the down-inlet half of Indian Arm. These planktonic occurrences probably are not usual. A crawling rather than swimming habit is indicated by the limbs' terminating in claws instead of natatory setae. Furthermore, Smith (1952) reports specimens occurring on the hydroid *Obelia* near the surface of the water at Departure Bay, B.C. Probably the specimens collected had been swept from their normal habitat and set adrift.

DIAGNOSIS

Terminal claw of second antenna striated and broad for most of its length; toward the tip it curves and then abruptly straightens to form a naked tip (Fig. 1). Third joint of the seventh limb densely pilose along the distal half of its anterior margin. (After Smith, 1952.)

DISCUSSION

Smith's (1952) description of *Paradoxostoma striungulum* corresponds well to the four adult specimens (3 males and 1 female) found in the Indian Arm material. Smith described and illustrated the shell, first antenna, second antenna, third walking leg (herein called the seventh limb) and the copulatory appendage (the penis).

Because the four specimens available from Indian Arm had been compressed in preparation, no adequate shell measurements were obtained. Lengths of

the compressed shells were about 0.40 mm for the males and 0.59 mm for the female, less than the 0.57 and 0.64 mm reported by Smith.

Figure 2 supplements the drawing by Smith (1952) and clarifies the external morphology of the penis. Smith stated that the flagellum (exopodite) of the second antenna was articulated in two places. A third, more distal articulation was indicated in the specimens from Indian Arm (Fig. 1). In the female and in two of the males this was barely perceptible, but in the third male it was as distinct as those articulations found proximally. This additional articulation is regarded as a variation, previously unobserved within the species. In other characters agreement with Smith's description is close.

Suborder CYPRIDINIFORMES
Family CYPRIDINIDAE
Subfamily PHILOMEDININAE
Genus *Philomedes* Lilljeborg

Philomedes sp.

OCCURRENCE

A single male was collected at night in April at a depth of 50–55 m from near the mouth of Indian Arm, in water approximately 60 m deep.

DIAGNOSIS (MALE ONLY)

Endopodite of second antenna with four basal and two distal setae on the first segment and with a long hyaline, non-annulated seta on the third segment. Seventh limb with four distal and three marginal setae. Caudal furca with first, second, third, and fifth claws strong and the remaining six claws weak.

DESCRIPTION (MALE ONLY)

SHELL (Fig. 3). The shell is more or less oval and about 2 mm long. The anterior margin has a small rostrum and shallow rostral sinus; the posterior margin is partly straight, giving the shell a truncated appearance. The dorsal margin is less convex than the ventral margin. The surface of the shell is heavily pitted and bears sparsely scattered, fine setae; its margin is comparatively smooth and, especially anteriorly and posteriorly, possesses conspicuous setae.

FIRST ANTENNA (Fig. 4). Of the six segments of the first antenna, the first is without setae, the second has three, the third has two or three, and the fourth has five setae. In addition, at the junction of the fourth and fifth segments, there is a sensory seta (Fig. 4, **s.s.**) having a pilose swollen base and a bifurcate tapered tip. This seta is at least as long as the second segment. The fifth segment has one seta and the sixth has seven setae.

The sixth segment (Fig. 4, **6.**) possesses: three slender setae without filaments; two short, stout setae with several filaments protruding at an angle from one side; and two extremely long, stout setae (Fig. 4; **1.**, **1.**) having similar filaments, inconspicuously appressed to the side (filaments of these last two setae not shown in Fig. 4). One of the latter setae is slightly longer than the other and is almost three times the combined length of the five distal segments of the first antenna.

FIGURES 1–7

Paradoxostoma striungulum Smith

FIG. 1. Second antenna, medial view.

FIG. 2. Penis and caudal furca, viewed from right.

Philomedes sp.

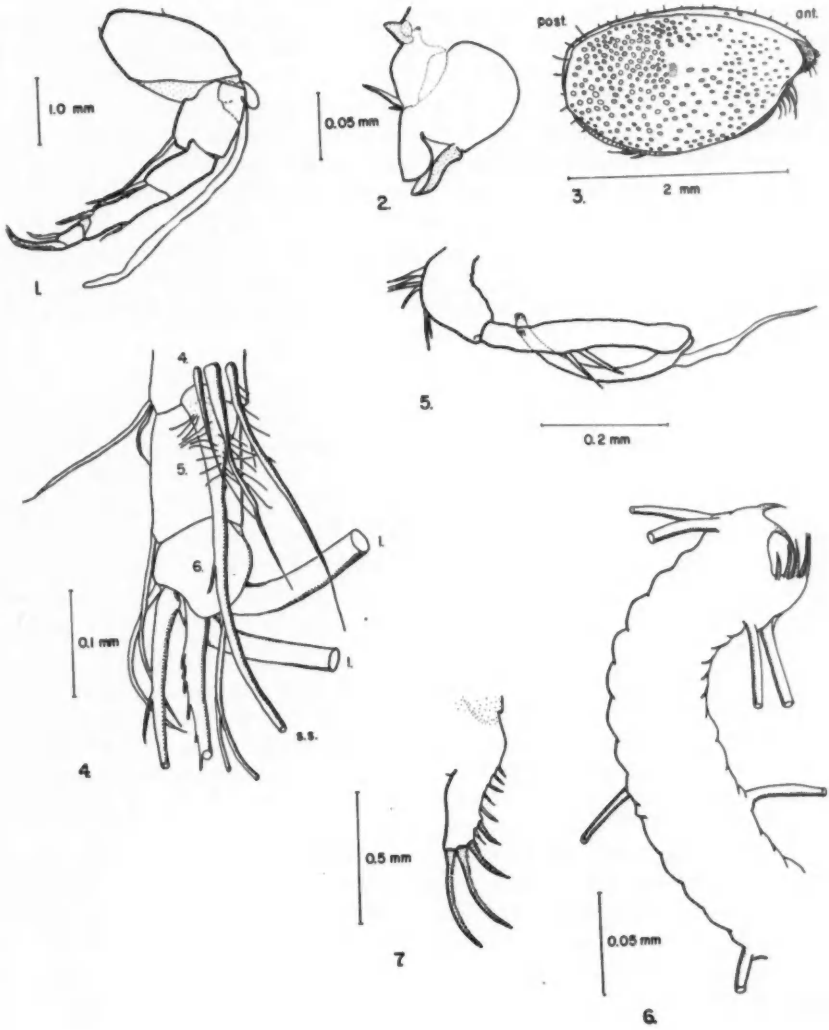
FIG. 3. Shell intact with animal, viewed slightly dorsally from right.

FIG. 4. Distal segments of first antenna, medial view (**s.s.** = sensory seta; **4**, **5**, **6**, = segments; **l.**,**l.** = longer setae).

FIG. 5. Endopodite of second antenna, medial view.

FIG. 6. Distal portion of seventh limb.

FIG. 7. Caudal furca, viewed from left.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ENDOPODITE OF SECOND ANTENNA (Fig. 5). The three-segmented endopodite forms a clasping organ, the third segment being flexed back onto the second. The first segment possesses four setae near its base and two others further distally. The second segment is straight and, midway along the surface opposed to the third segment, possesses two setae, each between two- and three-tenths as long as the parent segment. The third segment is curved; at its base is a transparent seta about three-quarters as long as the second segment; at its distal end is a pair of minute, yet distinct, spines.

SEVENTH LIMB (Fig. 6). The distal end of the seventh limb resembles a pair of gaping jaws with two teeth on one jaw and six on the other. Adjacent to this structure are two diametrically opposed pairs of distal setae. Proximally to these are three marginal setae.

CAUDAL FURCA (Fig. 7). Each furca is armed with ten claws. The first, second, third, and fifth claws are distinctly curved and heavily chitinized; the fourth and the sixth to tenth claws are almost straight and nearly transparent.

DISCUSSION

The preceding description is based on only one mature male specimen. Appendages chosen for illustration were those which provided comparison with the somewhat similar species, *Philomedes carcharodonta* Smith (1952), also found in B.C. waters.

The shell, frontal organ, first antenna, and caudal furca of *Philomedes carcharodonta* agree closely with those of the specimen from Indian Arm. Smith's diagnosis, however, omits mention of the texture of the shell (which is heavily pitted in the Indian Arm form) and differs from the Indian Arm specimen with regard to the setae on the "exopodite" (herein called the endopodite) of the second antenna and the setae on the seventh appendage (seventh limb).

In *Philomedes carcharodonta* the first segment of the endopodite of the second antenna has five setae basally and one anteriorly (Smith, 1952). The second segment is said to have a long annulated seta on its distal margin. The origin of this seta would appear, however, to have been misinterpreted by Smith since, in the generic diagnosis, it is placed at the proximal end of the third segment (Skogsberg, 1920).

In the Indian Arm specimen (Fig. 5), the first segment possesses four setae basally and two disto-anteriorly. A long seta at the proximal end of the third segment is not annulated, but entirely hyaline. Its position on the third segment agrees with that in the generic diagnosis.

The seventh limb of *Philomedes carcharodonta* has four distal and eight marginal setae (Smith, 1952). In the Indian Arm specimen (Fig. 6) this limb possesses four distal setae but only three marginal ones.

So far as known, no other species of *Philomedes* has the same arrangement of strong and weak claws on the caudal furca that occurs in both *Philomedes carcharodonta* and the Indian Arm specimen (Fig. 7). In some there is an antero-posterior gradation of claws from strong to weak; in others there is an inter-

mingling of strong and weak. Often in the latter arrangement, a weak third claw is placed with strong first, second, and fourth claws. The possession of strong first, second, third, and fifth claws with weak fourth and remaining claws, as found in *P. carcharodonta* and the Indian Arm specimen, does not seem to have been equalled in other species of *Philomedes* (Baird, 1850; Müller, 1894; Brady, 1907; Juday, 1907; Lucas, 1931; Rome, 1942; Smith, 1952; and Kornicker, 1958).

Although similar in general description and in the unusual arrangement of their furcal claws, *Philomedes carcharodonta* Smith and the specimen from Indian Arm are shown to differ in the setation of the endopodite of the second antenna and the setation of the seventh limb. The Indian Arm specimen could possibly be a variant of *P. carcharodonta*, or it could be a new species. To establish its identity would require a knowledge of the variability of the characters discussed. With only the one specimen available, this variability could not be estimated and consequently the specific identity of the specimen has had to be left open.

Suborder HALOCYPRIFORMES
Family HALOCYPRIDAE
Genus *Conchoecia* Dana

Conchoecia elegans Sars

Conchoecia elegans Sars, 1965[5]
Paraconchoecia gracilis Claus, 1891

For descriptions see Müller (1906a), Skogsberg (1920), Sars (1928); for an extensive bibliography see Skogsberg (1920).

DISTRIBUTION

Conchoecia elegans was regarded by Elofson (1941) as being probably cosmopolitan. It has been reported to occur in the Atlantic Ocean from 79°58′N to 55°S (Skogsberg, 1920), in the Indian Ocean from 13°02′N to 27°59′S (Müller, 1906a), and in the western Pacific Ocean at 0°17′S, 129°14′E and 4°30′S, 128°20′E (Müller, 1906b, p. 37). Locally, in the eastern Pacific, the species has been taken from the region of Vancouver Island, British Columbia (Smith, 1952).

OCCURRENCE

In May 1959, *Conchoecia elegans* was collected from various inlets of Vancouver Island (Muchalat, Alberni, Tofino, and Herbert Inlets) and the mainland of British Columbia (Knight Inlet, Bute Inlet, and Indian Arm). In 1960 it was obtained monthly from Indian Arm. Locations:

Muchalat — 49°40′N, 126°08′W
Alberni — 49°03′N, 124°51′W
Tofino — 49°12′N, 125°39′W
Herbert — 49°21′N, 125°57′W
Knight — 50°42′N, 125°49′W; 50°53′N, 125°39′W
Bute — 50°32′N, 125°00′W; 50°46′N, 124°54′W
Indian Arm — 49°25′N, 122°52′W and other stations (Anon., MS, 1959 and MS, 1961).

[5]Unseen.

DIAGNOSIS

Shell with two or three spines on postero-dorsal corner of right valve, with left asymmetric gland on postero-dorsal corner of left valve, and with right asymmetric gland on postero-ventral corner of right valve.

Frontal organ of female with capitulum and shaft joined at a level opposite the articulation of the second and third segments of first antenna.

Principal seta of male first antenna with shield-shaped "oval organ" succeeded by a distal portion bearing two opposed rows of four or five spines each and tapering without appearing tubular or thin-walled. Endopodite of male second antenna with terminal setae (**f** and **g**) distinctly different in length and not enlarged at bases. Penis "S"-shaped. (After Müller, 1906a, and Skogsberg, 1920.)

DISCUSSION

Probably the only species which can be confused with *Conchoecia elegans* are *C. discophora* Müller and *C. pseudodiscophora* Rudjakov. These three species have in common a characteristic "S"-shaped penis and a peculiar "oval-organ" adorning the principal seta (seta **e**) of the first antenna of the male (Müller, 1906a; Rudjakov, 1962). *Conchoecia elegans* and *C. discophora* have one or more well-developed spines on the postero-dorsal corner of the right valve, a characteristic which distinguishes them from *C. pseudodiscophora* (Rudjakov, 1962).

Conchoecia elegans and *C. discophora* may be distinguished on the structure of the principal seta of the male first antenna, the endopodite of the male second antenna, and on the relative lengths of frontal organ and first antenna in the female (Müller, 1906a). In the Indian Arm material the principal seta of the male first antenna does not terminate in a tubular, thin-walled portion (Müller, 1906a, pl. XIII, fig. 8 and 9); the terminal setae (**f** and **g**) of the endopodite of the male second antenna are distinctly different in length and do not possess swollen bases (Müller, 1906a, pl. XIII, fig. 3 to 7); and in the female, the first antenna extends farther anteriorly than does the junction of the capitulum and shaft of the adjacent frontal organ. By these three features the Indian Arm material can be identified with *C. elegans* Sars.

Although a few discrepancies were found, between the Indian Arm specimens and the descriptions of *Conchoecia elegans* given by Skogsberg (1920) and by Müller (1906a), agreement is remarkably good considering the number of minute details represented in the comparison (Skogsberg, 1920, pp. 624–31). The differences between the present material and previous descriptions may be listed under two categories, as follows:

1. Those due to omissions in previous descriptions:

a. Presence of spines distal to the oval organ of the male first antenna (omitted in Müller, 1906a, p. 69). These spines in the Indian Arm specimens are similar to those described by Skogsberg (1920, fig. CXVIII, no. 15).

b. Occurrence of a dorsal seta on the female first antenna (not confirmed by either Müller, 1906a, or Skogsberg, 1920). In females from Indian Arm, the dorsal seta is present on one or both of the first antennae about as often as not.

c. Occurrence of sexual dimorphism in the structure of the mandible (mentioned by neither Skogsberg nor Müller). In the Indian Arm specimens both the coxa and basis of the male mandible are longer (measured along their anterior edges) than those of the female. Also the basis in the male is longer relative to the coxa than it is in the female. The endopodial segments do not show such sexual dimorphism.

2. Those regarded as natural variations:

a. Difference in the ratio of length to height of the shell. Specimens from Indian Arm and the other B.C. inlets (see under Occurrence, above) have shown a ratio of 2.2:1. Müller (1906a) gives the ratio as less than that for *Conchoecia discophora* (i.e. less than 2.5). Skogsberg states it to be 2.6.

b. Difference in shell length. Shell lengths of males from Indian Arm and the other B.C. inlets measure from 1.4 to 1.7 mm. Males from the Atlantic and adjacent northerly Antarctic waters are similar, measuring from 1.2 to 2.0 mm, whereas males from Skagerrak, Kattegat, Lofoten and the Arctic Ocean and the most southerly station in the Antarctic are larger, measuring from 1.8 to 2.3 mm (Skogsberg, 1920).

c. Occurrence of a certain process on the postero-dorsal corner of the right valve. The process is not present in Indian Arm specimens or in males from the Antarctic Ocean (Skogsberg, 1920, fig. CXVII, no. 4) but it is present in males from Scandinavian waters (Skogsberg, 1920, fig. CXVII, no. 3).

d. Difference in the ratio of length of the capitulum to depth of the second segment of the first antenna in the male. Specimens from Indian Arm and the other inlets have the ratio of 1.4:1, with the capitulum the larger; in Skogsberg's material the ratio was about 1:1 (Skogsberg, 1920).

These several discrepancies are regarded as relatively trivial in number; they are possibly of little diagnostic significance at the species level, and are considered to provide insufficient reason to doubt that the Indian Arm material is *Conchoecia elegans* Sars.

Conchoecia alata minor n. subsp.

OCCURRENCE

Specimens were collected in May 1959 from Bute, Knight, and Muchalat Inlets. In 1960, specimens were collected monthly from Indian Arm. Locations:

Knight — 50°42′N, 125°49′W
50°53′N, 125°39′W
Bute — 50°32′N, 125°00′W
50°46′N, 124°54′W
Muchalat — 49°40′N, 126°08′W
Indian Arm — 49°25′N, 122°52′W and other stations (Anon., MS, 1959 and MS, 1961).

DIAGNOSIS

Shoulder vault of shell raised, with dorsal and lateral surfaces meeting to form right-angled ridges prominent in the anterior half of shell and gradually reduced to obscurity in posterior half. Shell with left asymmetric gland on postero-dorsal corner of left valve and right asymmetric gland on postero-ventral corner of right valve. Posterior margin of each valve with three or, more usually,

four groups of lateral glands; and in the male, with also a group of dorso-medial glands.

Principal seta of male first antenna with two adjacent rows of 25–40 processes per row. Each process consists of a chitinous "T"-shaped framework having a body of hyaline material on the distal side only.

DESCRIPTION

SHELL (Fig. 8–11). The length of the female shell ranges from 2 to 2.5 mm (Fig. 22) and averages about 1.14 times that of the male. The height of the male shell is about 0.56 of its length and that of the female about 0.59. In both sexes there is a depression about midway along the dorsal surface of the shell; in the female the height of the shell is greater posteriorly whereas in the male it is nearly the same anteriorly and posteriorly of this depression (*cf.* Fig. 8 and 9).

The anterior half of the shell forms an angular shoulder vault over the first segments of the second antennae. Dorsally the shoulder vault is flat; anteriorly it forms part of the rostrum; on either side it meets the lateral surface at right angles to form a ridge (Fig. 10 and 11). Posterior to the bases of the second antennae, each ridge converges medially and blends into the dorso-lateral surface, and the dorsal surface becomes closely contoured to the body. The postero-dorsal extremities of both valves may be either rounded or bluntly pointed.

SHELL GLANDS (Fig. 12). The locations of the two asymmetric glands (Fig. 12, **asm.**) are those usual for most species of the genus (Müller, 1912, fig. 17, p. 59). The left gland is present beside the hinge-line where it opens by a pore near the postero-dorsal corner of the left valve; the right gland is located at the postero-ventral corner of the right valve where it opens on the shell edge. These glands are similar in both sexes.

In the male, the postero-dorsal extremity of each valve possesses a dense cluster of medial glands, the dorso-medial group (Fig. 12, **d-m.**). This group of glands is absent in the female.

In both sexes other medial glands (Fig. 12, **m.**) of a less conspicuous nature occur singly, or less commonly in pairs, along most of the margin of the shell. These medial glands are distinguishable from other glands present on the posterior margin in that their pores are distinctly recessed from the edge.

Seven or eight groups of lateral glands occur on the posterior margin (Fig. 12, **lat.**), three or four on each valve. One is situated within the dorsal three-tenths of the posterior margin and the remaining two or three are located within the ventral four-tenths. The number of ventral groups are, with almost equal frequency, (1) two on the right valve and three on the left, (2) three on the right and two on the left, or (3) three on each valve. Usually there is only a single group dorsally, but occasionally there may be two, one or both of which may be small. Ducts of the lateral glands appear as tubes lying side by side, opening very close to the edge of the shell.

FRONTAL ORGAN (Fig. 13 and 14). In the male (Fig. 13) the distal segment of the shaft is about one and one-half times as long as the proximal segment of the shaft and slightly longer than the capitulum. It joins the capitulum in the

vicinity of the third segment of the first antenna. The capitulum is ventrally inclined, dorso-ventrally flattened and roughly uniform in depth; it tapers in width from a broad base to a more or less bluntly pointed tip. Short, distally directed setae occur on the proximal half of its dorsal surface, on the proximal two-thirds of its lateral surfaces, and on the proximal three-quarters of its ventral surface. In addition, a few setae may occur toward the tip, along the mid-line of the ventral surface.

In the female, the frontal organ (Fig. 14) is relatively straight. Its shaft is undivided and joins the capitulum just beyond the tip of the first antenna. The capitulum is about two-thirds the length of the shaft and, except at its slightly sinuous and acutely pointed tip, is more or less uniform in depth. Unlike the capitulum in the male, that in the female appears to be laterally compressed. Setae on the capitulum of the female frontal organ have a similar distribution to those of the male, but are considerably coarser, being almost spine-like.

FIRST ANTENNA (Fig. 13 and 14). In the male (Fig. 13), the second segment of the first antenna bears a retinaculum; the first and third segments are without setae; the fourth possesses setae **a** and **b**; and the fifth bears setae **c**, **d**, and **e** (terms from Skogsberg, 1920).

Seta **a** (Fig. 13) is bent sharply forward, then downward, and curved backward and upward so that it resembles a sickle. The perpendicular distance between the base and the most distant part of this contorted seta approximates the length of seta **c**. Setae **a** and **c** are hyaline, scarcely tapered, and rounded at their tips.

Setae **b**, **d**, and **e** are each chitinized, tapered, and approximately one and one-half times as long as the combined segments of the first antenna. Both **b** and **d** are distinctly bent at about seven-tenths of their lengths. Seta **b** is bare or has a few inconspicuous fine bristles along the outer surface of the bent portion. Seta **d** has a row of 10–30 distally directed, moderately spaced, simple, slender spines located at a position just proximal to the bent portion (Fig. 13, **x---x**). Between four and seven-tenths of the length of seta **e** (the principal seta) there are two adjacent rows each of 25–40 processes (Fig. 13, *---*).

Each of these processes has a chitinized framework which, in profile, resembles a capital "T" standing nearly upright or tilting slightly toward the distal end of the seta (Fig. 15). A body of hyaline material lies between the distal extension of the "T" and the body of the seta. Viewed at an angle perpendicular to the axis of the seta (Fig. 16), the process is seen to possess a broad and nearly straight outer edge, slightly indented on its upper (distal) surface.

In the female, a dorsal seta on the second segment has short fine bristles (Fig. 14, bristles not visible), and is about as long as the capitulum of the frontal organ. Setae **a**, **b**, **c**, and **d** of the male are represented in the female by four sensory setae, each of which is longer than the second segment of the first antenna, but shorter than the second to fifth segments combined. Seta **e** (the principal seta) is about three times the length of a sensory seta. It bears slender,

FIGURES 8–12

Conchoecia alata minor n. subsp.

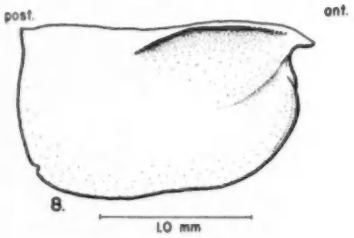
FIG. 8. Shell of male viewed from right.

FIG. 9. Shell of female viewed from right.

FIG. 10. Shell of male, dorsal view.

FIG. 11. Shell of male, ventral view.

FIG. 12. Posterior margin of opened shell of male, ventral view (**lat.** = lateral gland pores; **d-m** = dorso-medial gland pores; **asm.** = asymmetric gland; **m.** = medial gland pore).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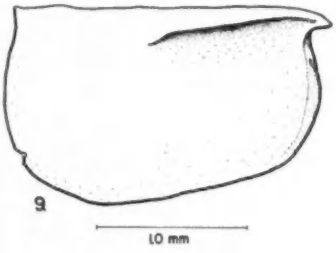
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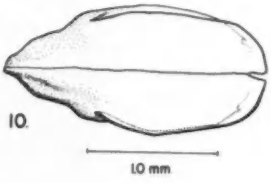
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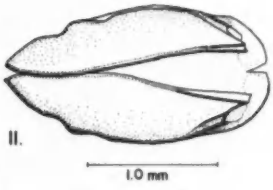
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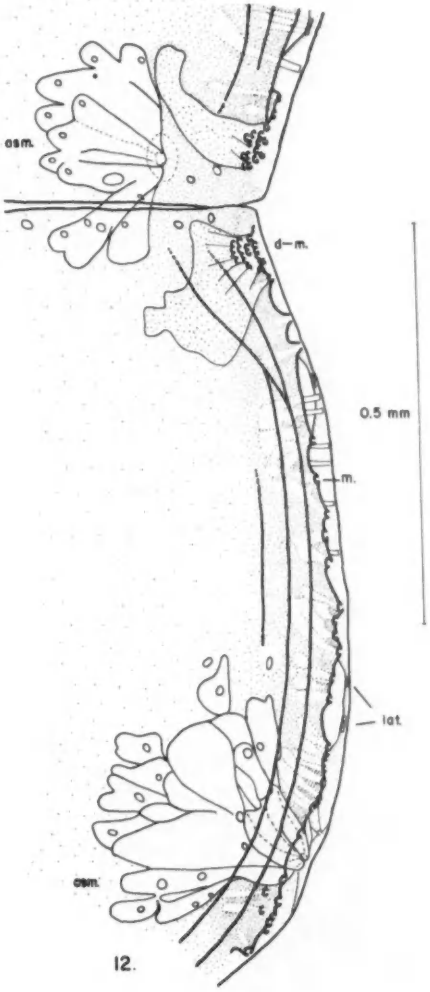
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FIGURES 13–18

Conchoecia alata minor n. subsp.

FIG. 13. Frontal organ and left first antenna of male viewed from right (**a**. to **e**. = setae, see text; **x**---**x** = equipment of seta **d**; *---* = equipment of seta **e**).

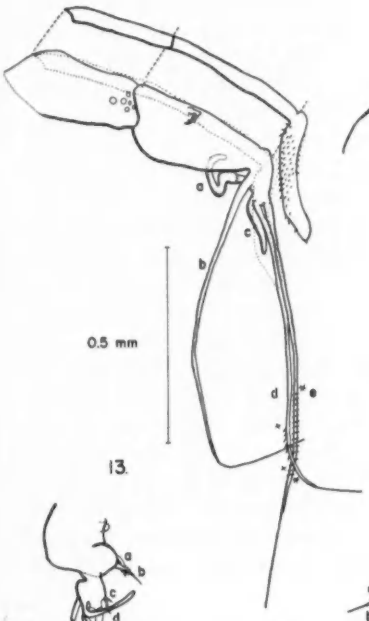
FIG. 14. Frontal organ and right first antenna of female viewed from left (**e**. = seta **e**).

FIG. 15. Portion of seta **e** of male first antenna equipped with processes.

FIG. 16. Process of seta **e** of male first antenna (freehand)

FIG. 17. Endopodite of left second antenna of male, medial view (**a**. to **j**. = setae, see text).

FIG. 18. Endopodite of female second antenna, medial view (**a**. to **j**. = setae, see text).



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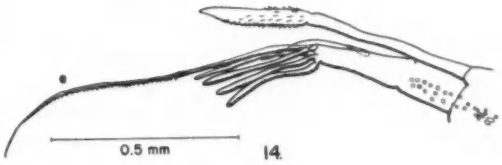

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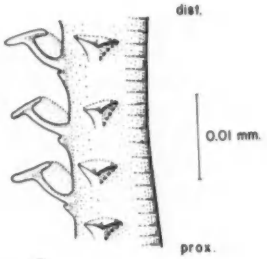

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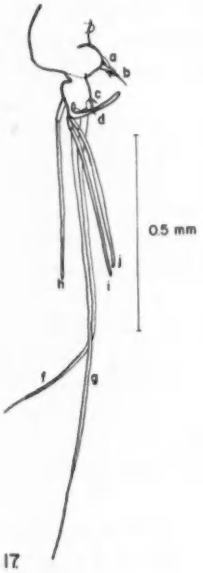

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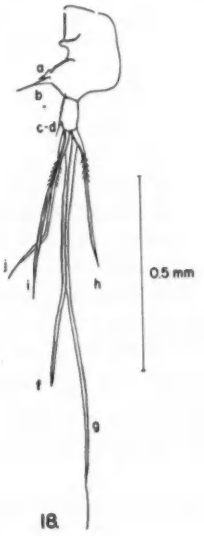

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moderately spaced, distally inclined fine bristles along its ventral surface, between one-third and three-quarters of its length.

ENDOPODITE OF SECOND ANTENNA (Fig. 17 and 18). In the male, the endopodite of the second antenna consists of three segments (in Fig. 17 terminal segmentation not clear). Of two mammillae present on the antero-dorsal surface of the first segment, the distal mammilla (with setae **a** and **b**) is wider than high and the proximal mammilla, or processus mammillaris (without setae), is higher than wide. In profile (laterally or medially), the proximal mammilla appears to have about one-quarter the area of the distal mammilla.

The second segment bears setae **c**, **d**, **e**, **f**, and **g** (Fig. 17). Seta **e** (not shown in Fig. 17) is a small, often inconspicuous spine located at the base of seta **f**. Seta **f** is about as long as the protopodite; seta **g** is longer and more chitinized than **f**, and is a little shorter than the combined lengths of the protopodite and the first segment of the exopodite. The distal portion of seta **f** forms a distinct bend and crosses seta **g** at about six-tenths of the length of **g**. Bristles on these two setae, whenever present, are sparse and inconspicuous.

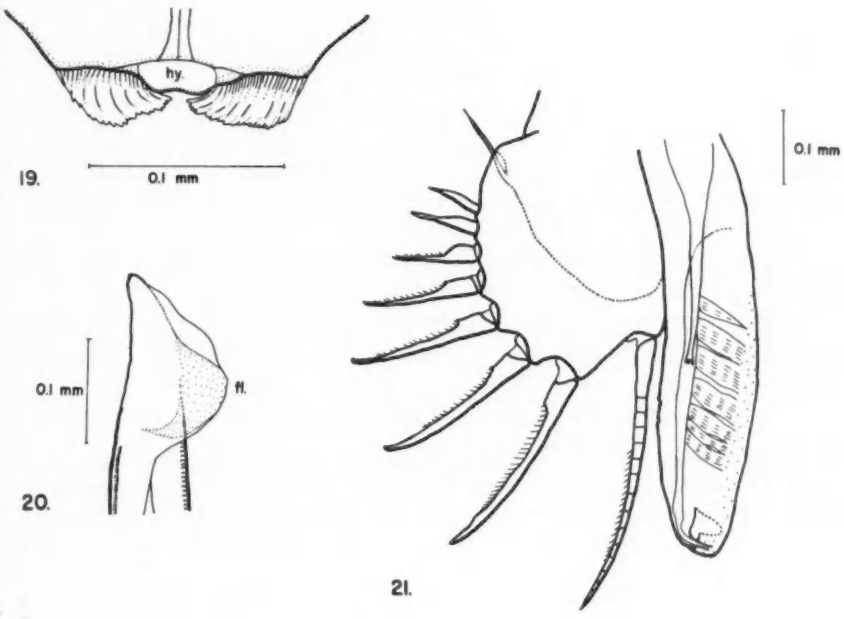
The third segment is swollen at the base and possesses a hook and three sensory setae **h**, **i**, and **j**. Each of these setae is about four-tenths as long as seta **g**. On the right second antenna the distal portion of the hook is about three times longer than the proximal portion (measured between the swollen segment proper and the angle of the hook) and is distinctly bowed and terminally cuspidate. On the left limb (Fig. 17) the distal portion is about four times the length of the proximal, is nearly straight, and possesses faint terminal cuspidation. Both portions of the hook of the right second antenna are longer and more heavily chitinized than those of the left.

In the second antenna of the female, the endopodite is two-segmented; setae **c** and **d** (of the male) are replaced by a single, distally directed spine (Fig. 18, **c-d**); seta **e** appears to be absent, or represented by a small, heavily chitinized nob under the base of seta **f**. Seta **f** is straight, chitinized, eight- to nine-tenths the length of protopodite, and possesses a few scattered fine bristles. Seta **g** is straight and slightly longer than the protopodite; it is more heavily chitinized than **f**, and possesses no bristles.

Each of the sensory setae **h**, **i**, and **j** is one-half (or slightly less) as long as seta **g** and possesses conspicuous short bristles on its basal third, but none distally.

LABRUM. The posterior margin of the hyaline plate (Fig. 19, **hy.**) found between the two comb-like structures on the postero-ventral margin of the labrum (the labral lamina of Iles, 1961), is nearly straight; there is only shallow indentation.

MANDIBLE. The relative proportions of the five segments of the mandible are not noticeably different between males and females. When cleared of muscles, the "anterior dorsal flange" of the coxa (Iles, 1961) is seen to be recessed from the proximal tip (Fig. 20, **fl.**). Of the three toothed ridges of the masticatory endite of the coxa, the toothed edge has 10 teeth, the distal tooth-list has 13–16, and the proximal tooth-list has 10–15 teeth.



FIGURES 19–21

Conchoecia alata minor n. subsp.

FIG. 19. Posterior edge of labrum, ventral view (**hy.** = hyaline plate, see text).

FIG. 20. Proximal extremity of mandible, medial view (**fl.** = anterior dorsal flange).

FIG. 21. Penis and caudal furca, viewed from right.

SIXTH LIMB. The exopodite consists of four segments and is sexually dimorphic. In the male it is about one and one-third times as long as in the female, measured along its ventral edge. Proportions of first, second, and third segments are respectively about 10:5:7 in the male, and about 10:7:10 in the female. In the male any one of the terminal setae is almost as long as the ventral edge of the exopodite, whereas in the female the longest terminal seta is about half as long as the ventral edge of the exopodite.

PENIS (Fig. 21). The penis is almost straight and is directed more or less ventrally. The anteriorly directed copulatory appendage, (Fig. 21, *broken line*), situated on the right side near the tip of the penis, is almost as broad at its base as it is long. Its length is slightly more than half the breadth of the portion of the penis to which it is attached.

Six to eight transverse or slightly oblique muscle bands are located in the proximal four-fifths of the penis.

CAUDAL FURCA (Fig. 21). Posterior to the claws, and partly imbedded between the furcae, is a single (unpaired) seta, at least as long as the seventh claw.

STATION "P" SUBSPECIES OF *CONCHOECIA ALATA*

In September 1959, two adult specimens, one of each sex, were collected at the Pacific Ocean Weather Station "P" (50°N, 145°W). These specimens were about one-third larger than those from the British Columbia inlets, but conformed well to the above diagnosis. Shell-length measurements of the specimens from Station "P" and the B. C. inlets are compared in Fig. 22. Among the populations from the inlets, the intervals of three standard deviations were found to overlap (Fig. 22), indicating that the mean shell lengths of these populations are probably quite similar. The shell lengths of the two specimens from Station "P", however, were greater than three standard deviations above the sample mean for any of the inlet populations. This suggests that the Station "P" specimens were of a larger mean size, which may be a characteristic of a distinct "oceanic" population. Thus, specimens from the inlets and from Station "P" are considered to be distinct from one another.

DISCUSSION

Because the material described has more than one group of lateral glands on at least one valve of the shell, it may be included in Müller's (1906a) *alata* group of the genus *Conchoecia*. Müller (1906a, c) has included (and described) five species in this group, namely, *Conchoecia leptothrix*, *C. valdiviae*, *C. hettraca*, *C. belgicae* and *C. alata*. *Conchoecia leptothrix* and *C. valdiviae* were regarded by Müller (1906a) as being "isolated", but he retained them within the group for want of better classification. He regarded *C. hettraca* and *C. belgicae* as being more closely related to one another than to *C. alata* (Müller, 1906a, c).

The form described herein seems closer to *Conchoecia alata* than to *C. hettraca* or *C. belgicae*. *Conchoecia hettraca* and *C. belgicae* are related morphologically by possessing (1) lateral gland-groups only on the left valve and by having (2)

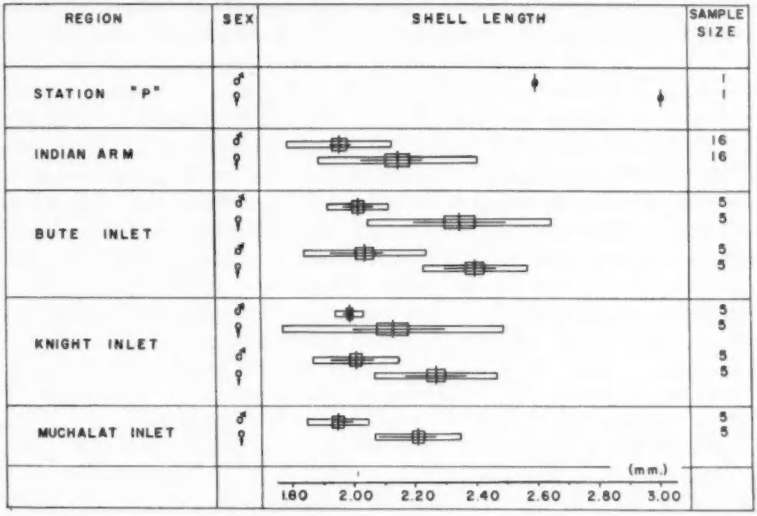


FIG. 22. Shell lengths of male and female specimens of the subspecies from Station "P" and of *Conchoecia alata minor* n. subsp. from certain B.C. inlets. Statistics: mean (vertical line), range (horizontal line), intervals of one standard error (shorter bar) and of three standard deviations (long bar) on both sides of the mean.

peg-like processes on the principal seta of the male first antenna. On the other hand *C. alata* and the present material have in common (1) groups of lateral glands on both left and right valves, and (2) processes of superficially "T"-shaped profile on the principal seta of the male first antenna. This evidence suggests that *C. alata* is related to the present form about as closely as *C. hettraca* is to *C. belgicae*.

Recently *Conchoecia alata* was divided into *C. alata alata* Müller and *C. alata major* Rudjakov on the bases of the angle of the postero-dorsal corner of the shell and the size of the shell (Rudjakov, 1962). The postero-dorsal corner of each valve in *C. alata major* is obtuse, with spines either not expressed or only developed slightly, whereas, in *C. alata alata* the corners are drawn out into distinct spines (Rudjakov, 1962; Müller, 1906a).

Specimens from the B.C. inlets and from Station "P" not only differ from *Conchoecia alata alata* in having obtusely shaped postero-dorsal corners on the shell (as in *C. alata major*), but also in having neither wing-like extensions of the shoulder vaults of the shell nor a maximum of three groups of lateral glands on the posterior margin of the shell (as in *C. alata alata* and *C. alata major* — Müller, 1906a; Rudjakov, 1962). Furthermore, these specimens differ from *C. alata alata* in the structure of the processes of the principal seta of the male first antenna. Apparently *C. alata alata* is morphologically more distant from the present material than it is from *C. alata major*.

Müller (1906a) describes the chitinous framework in the processes on the principal seta of the male first antenna of *C. alata alata* as being like a "mushroom cap" bounded by *two* delicate membranes which produce "apparent wing-like widenings" of its stem. In his figure (fig. 7, pl. XXIX), the shape of each membrane is convex and would appear to enclose hyaline material. In the present specimens, on the other hand, the framework resembles a "bracket fungus" (Fig. 16) bounded by hyaline material only on the *one* side toward the distal end of the seta (Fig. 15); a membrane has not been observed. This difference in distribution of hyaline material, along with differences in shell shape and lateral gland arrangement, serves to distinguish *C. alata alata* from the present material.

Structure of the processes of the principal seta of the male first antenna of *Conchoecia alata major* was not described by Rudjakov (1962). Along those features which he did treat, the following were different from the present material. The base of seta **h** is considerably dilated in *C. alata major* (Rudjakov, 1962, pl. 14, fig. a), whereas in the present material it appears as in *C. alata alata* (Müller, 1906a, pl. XXIX, fig. 4 and 10). The number of teeth on the proximal tooth-list varies from 17 to 20 in *C. alata major*, whereas from 10 to 15 occur in the specimens from Indian Arm. These differences plus those concerned with the extension of the shoulder vault and the number of groups of lateral glands of the shell constitute evidence that *C. alata major* is somewhat different than the present material.

As previously noted, the specimens from the British Columbia inlets are one-third smaller than those from Station "P" (Fig. 22). The shell lengths of specimens from the inlets resemble those of *C. alata alata* whereas the shell lengths of specimens from Station "P" resemble those of *C. alata major* (Müller, 1906a; Rudjakov, 1962):

	Male	*Female*
C. alata alata	1.8 – 2.05 mm	2.1 – 2.4 mm
C. alata major	2.53 – 2.83 mm	2.93 – 3.25 mm
Inlet specimens	1.93 – 2.10 mm	2.00 – 2.50 mm
Station "P" specimens	2.60 mm	3.01 mm

Thus on the basis of size *C. alata major* is separated further from specimens of the inlets than it is from specimens of Station "P".

Because they are structurally identical except for size, specimens from the inlets and from Station "P" are considered to be very closely related. Although difference in size would make direct interbreeding by copulation improbable, a gradient of interbreeding populations could possibly exist between the extremely small specimens of the inlets and the extremely large specimens out in the ocean. In any case the amount of separation of these two populations is at least subspecific. The population represented by specimens from Station "P" is either a subspecies distinct from *Conchoecia alata major* or a variant of that subspecies. The population represented by specimens from the inlets is proposed to be a new subspecies, *C. alata minor*.

Conchoecia alata alata has been collected in the Atlantic Ocean between 25°35′N (Barney, 1921) and 30°06′S (Müller, 1906a); and in the Indian Ocean

from north of 4°05′S (Müller, 1906a; Cannon, 1940). In the Atlantic where its distribution is fairly well known (Müller, 1906a; Barney, 1921; Iles, 1953), *C. alata alata* appears to be limited between 30°N and 30°S.

Conchoecia alata major has been collected in the northwestern Pacific off the Kurile Islands from 43°N, 149°W to 49°N, 159°W (Rudjakov, 1952). The *C. alata* taken by Tchindonova (1959) from either the Kurile-Kamchatka region or further south (precise location not given) is probably *C. alata major*. The present material was collected in the northeastern Pacific: the large subspecies from 50°N, 145°W; the small one, *C. alata minor*, from the inlets of British Columbia (*see* Occurrence). It seems that study of the distribution of morphological variation in *C. alata* across the Pacific Ocean might reveal the evolution of a series of subspecies more or less effectively separated by distance or environment.

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Cooking Method and Palatability of Frozen Cod Fillets of Various Qualities[1,2,3]

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ABSTRACT

Cooking method modified the taste and texture scores of frozen cod fillets of various qualities. All methods gave high scores with good quality fish, but on samples with frozen storage deterioration, much better discrimination between quality levels was shown by baking and steaming than by frying; texture showed greater differences than taste. Initial quality levels of the fillets prior to freezing had little effect on scores or on the subsequent deterioration of the stored frozen product. Thus baking or possibly steaming is the best cooking method for detection and comparison of quality changes on storage. Frying is the method of choice for the consumer if product quality is in doubt, but any method may be used for a top-quality product.

INTRODUCTION

While good cooks adapt their methods of preparation and of cooking to the type and quality of the material at hand, little attention is usually paid to the manner in which the cooking procedure selected in taste panel testing of various foods may affect the results.

Various modifications of the three basic cooking procedures, baking, steaming and frying, have been used in preparation of samples for taste panel testing. Some workers have recognized that the cooking procedure may affect the quality level of the final cooked dish (Morton and Dyer, 1956; Carver and Steinberg, 1959; Baldwin *et al.*, 1962). However, little comparative study of the relative effects of method of cooking on texture, taste or other attributes of the product or on the ability of the panel to detect differences in quality has been undertaken.

A preliminary investigation (Dyer, Laishley, Fraser, Idler and MacCallum, unpublished) indicated the possibility that steaming may not be as discriminatory as baking in distinguishing differences in better quality frozen cod.

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The importance of the role of taste testing in evaluating quality and in determining the factors influencing it is so great that further experiments were set up to clarify these questions.

In addition it was desired to determine the most suitable cooking procedure for use by the consumer with fish of various qualities.

In collaboration with the Information and Consumer Service, Department of Fisheries of Canada, Ottawa, the three basic cooking procedures, baking, frying, and steaming, were compared on frozen cod fillets of various qualities. Two aspects of quality were assessed: first, spoilage, principally bacterial, occurring prior to freezing; and secondly, deterioration due to storage of the frozen product.

MATERIALS AND METHODS

Initial Quality — Freshness

Three lots of cod fillets (*Gadus morhua*) were processed at a local fish plant. It was specified that each lot be representative of fish of a known degree of initial freshness, ranging from very fresh material free of perceptible spoilage (Grade I), through incipient spoilage (Grade II), to definitely spoiling fish (Grade III). The fish were organoleptically graded for quality by experienced Department of Fisheries inspectors according to the Department's specifications. The first lot of fillets, processed in April 1962, was cut from Grade I fish; the second lot, received in June, was of Grade II quality; the third lot was processed in October from Grade III fish. The definitions of these grades in relation to the physical and organoleptic qualities of the fish are similar to those described by Castell *et al.* (1958).

The fillets were packed in 1-lb waxed, window-type cardboard packages, overwrapped with cellophane, machine sealed, and frozen in horizontal plate freezers. They were then packed in cardboard cartons holding 12 1-lb packages and transported immediately to the laboratory for frozen storage in thermostatically controlled cabinets.

Initial Quality — Frozen Storage Deterioration

Half of each lot was stored (A) at –26°C (–15°F) for 4 weeks; the other half was divided equally for storage (B) at –12°C (+10°F) for 2 weeks followed by storage at –26°C for 2 weeks, and (C) at –9°C (+15°F) for 4 weeks. Half of the samples stored at (A) were intended for use as "known" controls during the taste-panel testing.

These three storage conditions were selected to yield samples representative of good, medium, and poor frozen-storage qualities. No measurable change should result from frozen storage under condition (A); condition (B) would be expected to yield a product of intermediate quality, since storage at elevated temperatures for short periods of time causes considerable loss of quality; under condition (C) marked deterioration, approaching rejection levels, could be expected to occur (Dyer, 1957; Dyer *et al.*, 1957 a, b; Dyer and Dingle, 1961).

Any possible deterioration which might occur during thawing was avoided in the present work by cooking and by analyzing samples directly without prior thawing.

At the conclusion of the 4-week storage period the samples were packed in fibreglass insulated cartons containing dry ice and shipped to the Department of Fisheries Test Kitchen in Ottawa by air-express for taste testing. The temperature when opened on arrival was always –23°C or below, and extensive experience with this method of packing shows that temperatures after the period of time involved usually range from –23 to –40°C.

At Ottawa, the fish were placed in storage near –18°C (0°F) for the 7–10 days required to complete the cooking tests. A few samples were retained at Halifax for analysis.

Chemical Tests

As an objective measure of initial quality the trimethylamine (TMA) content of the fillets was determined by the colorimetric procedure of Dyer (1959).

Cooking Methods

Standardized procedures were developed for the three basic cooking methods. The baking procedure was based on that of Dyer and Dyer (1949) and Dyer and Morton (1956). The steaming procedure was similar to that used by Shewan *et al.* (1953).

Baking

The frozen 1-lb fillet blocks were each cut into 10 equal pieces. All samples to be served on a panel were placed in a lightly greased aluminum baking pan (30 × 45 × 5 cm) and baked, without prior thawing, for 20 min in a thermostatically controlled Garland Institutional oven set at 260°C (500°F).

Steaming

Servings were cut as above from the frozen fillet blocks and placed in individual casseroles covered with a double layer of aluminum foil secured by an elastic band. The casseroles were placed in a boiling water bath for 25 min.

Frying

To facilitate breading, the fillet blocks were placed in a refrigerator for 5 hr before preparation. They were then dipped in milk, rolled in dry bread crumbs, and pan-fried in Mazola oil at 190°C (375°F) for 3 min.

Taste Panel Assessment

Cooked samples of uniform size were served immediately to a panel of eight tasters, all of whom had received preliminary training in the taste panel assessment of frozen cod fillets. The samples were graded for texture, taste and overall acceptability using the taste panel technique, score sheet, and method of scoring previously described (Dyer and Dyer, 1949; Dyer and Morton, 1956). A "known" control sample, drawn from that portion of each lot stored under the best conditions available ((A) above), was served on each panel, along with three "unknown" samples representative of fish stored under the good (A), medium (B), and poor (C) conditions. Sample A thus served as an unknown or blind

control, as well as being representative of good conditions of frozen storage. Three panels were run on each set of samples using each of the three cooking methods, thus assuring a sufficient number of judgments per sample for statistical interpretation. Judges were asked to serve only once per half-day. The method of cooking was varied in random fashion so that a baking and a frying panel might be held one day, and steaming and frying the next. This also meant that samples for each cooking method came from different parts of a carton or from different cartons. It should also be noted that the panel members were given about equal preliminary training in each cooking method. The numerical scoring system ranges from 100 for the seldom attained perfect quality, through good, fair, borderline, not acceptable, to 0 for completely inedible quality. Freshly frozen good quality cod fillets cooked by baking usually rate above 70–80; samples are usually rated unacceptable at a level of 40 (Dyer *et al.*, 1962).

This system was followed as closely as possible with the steamed and fried samples.

RESULTS

The average TMA values at the end of the 4-week storage period were 1.0, 5.5, and 13.4 mg N per 100 g for the Grade I, II, and III cod fillets, respectively. Range of values determined in duplicate on three separate fillets was 0.6–1.6, 3.9–8.3 and 8.2–19.3, respectively, for the three grades. The average values found for the fillets of the three initial qualities, Grades I, II, and III, lie on the scale set up by Hoogland (1958) in his statistical analysis of data from studies of Castell *et al.* (1958) on the relationship between grades of quality and the TMA content. Frozen storage at the temperatures used effectively inhibits bacterial action and no further production of TMA occurs under these conditions (Dyer *et al.*, 1957a).

The texture and taste scores from the extensive taste testing of the various lots of frozen fish using the three basic cooking procedures are given in Table I. These show, first, surprisingly little difference between the scores of the samples of different initial freshness; secondly, much decreased scores in the frozen samples stored at –12°C (B) and a decrease to unacceptable levels in the case of the samples stored 4 weeks at –9°C (C) when baked or steamed. Thirdly, the taste panel acceptability scores of the frozen fillets stored under good conditions (A) are high for all cooking methods, but in the partly deteriorated samples scores are considerably lower following baking or steaming in comparison with frying. Fourthly, texture scores decrease much further than do taste levels in the samples exposed to poor frozen storage conditions when the samples are baked or steamed, though not when fried.

It will be noted that the scores for the unknown control are considerably lower than those for the known — as is often encountered in this kind of comparison (Peters and Slavin, 1962). The higher palatability level of the poorer stored frozen samples when cooked by frying is quite evident; sample C, which was rejected by the panel when baked, just barely accepted when steamed, is judged quite acceptable when fried. Further statistical calculations would appear to be unnecessary to show that frying does cover up many of the deficiencies

TABLE I. Texture and taste scores in frozen cod fillets of various qualities prepared by three cooking methods.

Sample		Baked		Steamed		Fried	
Initial freshness	Frozen storage condition	Texture[a]	Taste	Texture	Taste	Texture	Taste
Grade I	A (Known control)	91±(1.92)23	85±(1.79)23	88±(2.83)24	83±(3.33)24	89±(2.08)24	88±(2.32)24
	A (Unknown)	76±(4.25)24	70±(4.96)24	68±(4.22)23	63±(5.42)23	78±(3.27)23	75±(2.70)23
	B	48±(4.85)24	59±(4.60)24	80±(3.05)21	76±(3.27)21	70±(5.43)24	75±(4.34)24
	C	28±(3.19)22	46±(4.44)22	42±(4.23)24	51±(3.60)24	58±(4.91)24	58±(4.20)24
Grade II	A (Known control)	87±(3.44)24	87±(2.68)24	88±(3.05)21	82±(2.81)21	80±(5.09)24	89±(2.00)24
	A (Unknown)	64±(6.70)24	73±(4.91)24	68±(5.03)22	67±(4.65)22	75±(4.48)23	75±(4.22)23
	B	45±(5.77)24	55±(3.84)24	42±(5.62)23	51±(5.01)23	74±(4.62)23	74±(3.51)22
	C	25±(3.86)22	49±(4.48)22	36±(5.36)23	53±(4.46)23	59±(6.66)23	63±(5.41)23
Grade III	A (Known control)	79±(3.60)22	76±(4.29)22	86±(2.75)24	83±(3.48)24	92±(1.92)22	88±(2.59)22
	A (Unknown)	77±(4.10)23	72±(3.88)23	59±(4.74)24	62±(4.68)24	78±(4.98)23	80±(3.36)23
	B	65±(4.72)22	67±(3.90)22	66±(5.22)24	68±(3.85)24	65±(5.77)24	68±(4.21)24
	C	48±(5.49)22	50±(5.55)22	36±(5.22)24	45±(4.71)24	65±(6.10)23	67±(5.20)22

[a]Average values are given, with standard error of the mean in parentheses, followed by the number of judgments.

of samples suffering cold storage deterioration. This method therefore should not be used in taste testing designed to detect changes occurring on storage of frozen fish. On the other hand, for the consumer it is the method of choice if it is suspected that the product may not be top quality.

DISCUSSION

Freshness of Raw Material

Little difference either in texture or in taste scores is evident between the various degrees of freshness of the samples of the raw material used, whether stored under good or under poor frozen storage conditions, or with the cooking method used (Fig. 1). The fish of Grade III initial quality received scores similar to those of the Grade I fish, even though the TMA levels are indicative of considerable bacterial spoilage in the Grade III fish.

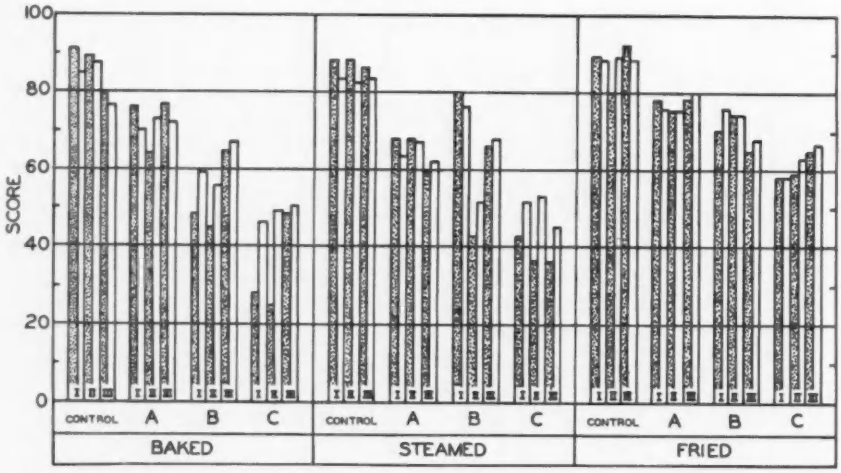

Fig. 1. Texture and taste scores in baked, steamed, and fried samples of frozen cod fillets of varying initial quality and stored under good, medium, and poor frozen storage conditions. *Initial quality*: Grade I, very fresh; Grade II, incipient spoilage; Grade III, definitely spoiling. Frozen storage quality: A, good; B, medium; C, poor (see Materials and Methods section). (Texture: hatched bars; taste: open bars.)

Probably two factors are involved. First, in a taste testing study of iced cod fillets in various stages of spoilage, Dyer and Dyer (1949) observed only a slight decrease in taste panel scores (on baked samples) from values of 60 in the fresh fillets to about 50 at a TMA level of 13. (Significant lowering of score occurred only at spoilage levels above 15–20 as TMA values.) Thus initial freshness did not greatly affect the taste acceptability, a result in agreement with the present work with the frozen product. Secondly, if Grade I quality fillets had been used as controls, slightly lower scores might have been obtained for the Grade II and III quality frozen samples, particularly those held under good frozen storage conditions.

This finding is not inconsistent with the fresh fish grading system based on dockside examination of the eviscerated iced fish prior to filleting in use in some areas. The system is designed to allow a margin of quality so that the iced fillets will remain edible during the time required for normal marketing.

Freshness and Cold Storage Quality

Does prefrozen quality affect changes occurring during frozen storage? Notevarp and Heen (1940) found greatly reduced frozen storage life of cod at either −12 or at −23°C when the fillets were held in ice for 3 or for 8 days prior to freezing in comparison with fillets frozen prior to rigor mortis. Also, Norwegian regulations state that frozen fish for export must be frozen before rigor mortis has passed. On the other hand, Dyer and Fraser (1959) and Fraser and Dyer (1959) found no detectable differences in protein extractable in salt solution, free fatty acids, or taste panel scores during frozen storage at −12 or −23°C in cod fillets from fish iced 1 or 8 days prior to freezing. Butler (1962) reports that after at least 6 months storage at −18°C, whitefish frozen after 6–8 days in ice were as good or better than fish frozen immediately on catching, thawed, and refrozen. Banks (1962) summarizes his experience by recommending that whitefish for freezing should have been no longer than 10–12 days in ice, preferably about half this time for high-grade packs.

It is evident from Fig. 1 that the samples of Grade II and III initial quality have not deteriorated further than the best quality Grade I fillets during frozen storage at −12°C (B) for 2 weeks, or during storage at −9°C for 4 weeks (C). In fact, they have a better texture score when cooked by baking (slightly better on steaming) with little difference showing in the fried samples.

The rate of quality loss may be calculated, and also storage life at the various temperatures, for comparison with previous results. If one assumes a negligible deterioration in 4 weeks at −26°C, then the average initial texture score of the Grade I, II and III fish is 72 (A). After 4 weeks at −9°C it has dropped to 34, a decrease of 1.36 units per day. If a score of 40 is taken as the dividing line between acceptable and unacceptable then the storage life at −9°C is only 25 days. For the fried samples the corresponding time is 54 days. If taste scores are used, the figures are 40 and 62 days, respectively. These times are comparable to the limit of 1½–2 months given by Dyer *et al.* (1957b).

At −12°C (2 weeks exposure) the figures are more variable: 23 and 74 days to unacceptability for texture scores of the baked and fried samples and 40 and 120 days for the corresponding taste values. These times are rather less than the 3½–4 months cited by Dyer *et al.* (1957b). It appears that the rate of quality loss is the same at −12°C as at −9°C. However, storage at −12° for 2 weeks was followed by further storage for 2 weeks at −26° and about a week at −18°, whereas the −9° samples were kept less than a week at the lower temperature prior to testing. Thus further deterioration has probably occurred during the 3 weeks at −23° or −18°C, resulting in greater apparent deterioration rates, as has previously been observed with frozen cod fillets exposed for a 2-week period to temperatures of −9° followed by low temperature storage (Dyer *et al.*, 1957a).

Because of the uncertainty of the score of the steamed sample (held at −26°C), the rates cannot be satisfactorily calculated. By taste testing of steamed samples, Gutschmidt (1962) indicates a storage life for lean fish of about 40 days for continuous storage at −12° and about 28 days at −9°C, values in the same range as found in the present work.

Texture and Taste

It is quite evident from Fig. 1 that texture scores are considerably lower than taste scores in the frozen samples stored under poor conditions (B and C) except in those cooked by frying. In the fried samples (Fig. 2) the scores for texture are equal to taste, but they are considerably lower in the steamed and even more so in the baked samples. The regularity of the curves shows that taste and texture scores fall off together with increasing frozen storage deterioration.

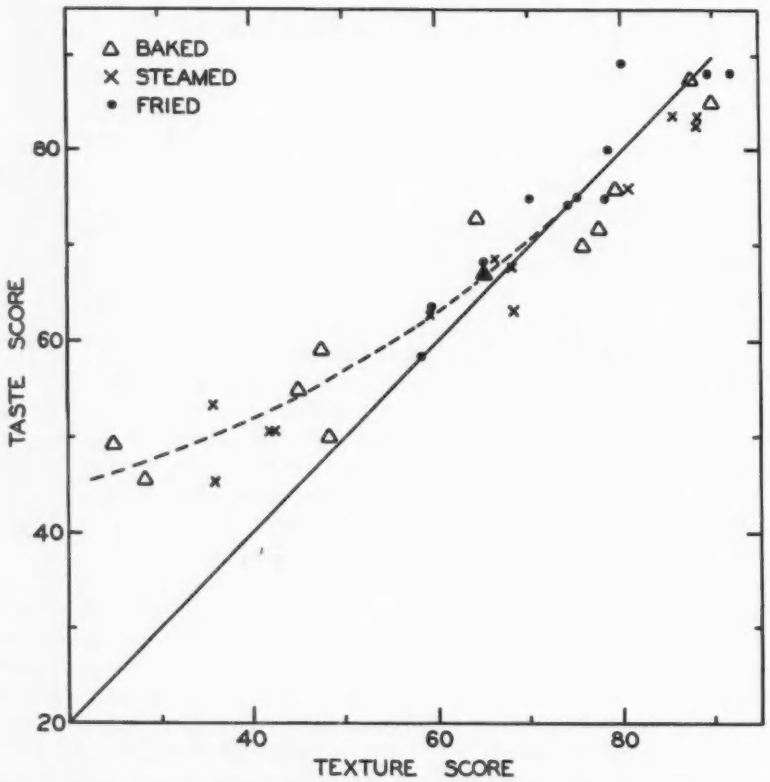

Fig. 2. Texture vs taste scores in baked, steamed, and fried frozen-stored cod fillets. Points represent the average of the combined scores of Grades I, II, and III samples at each frozen storage condition and cooking procedure. (If taste and texture scores are equal the points lie on the solid line (45°).)

Cooking Method and Frozen Storage Quality Levels

Figure 1 indicates that scores from the three cooking methods do not separate or discriminate to the same extent the various frozen storage qualities. This has been examined further by combining all scores of Grade I, II, and III fillets for each frozen storage quality and calculating the average and the standard error of the means for each frozen storage quality and each cooking method (Fig. 3). From these, the 95% confidence limits were obtained (s.e. $\times$ t .05) (Snedecor, 1956); the number of samples was 66–72, t .05 = 2.00. Briefly, this value represents the limits within which the means will fall in 95 out of every 100 times that the testing is repeated. It will be seen immediately from Fig. 3 that the texture scores for the fried samples overlap considerably and are not well separated. On the other hand, the corresponding values for the baked samples are well separated and show significant differences. Taste scores are similar, although differences are somewhat less. The tasters remarked that they found more difficulty in scoring the fried fish; there was less difference between the samples, a finding which is reflected in the scores assigned.

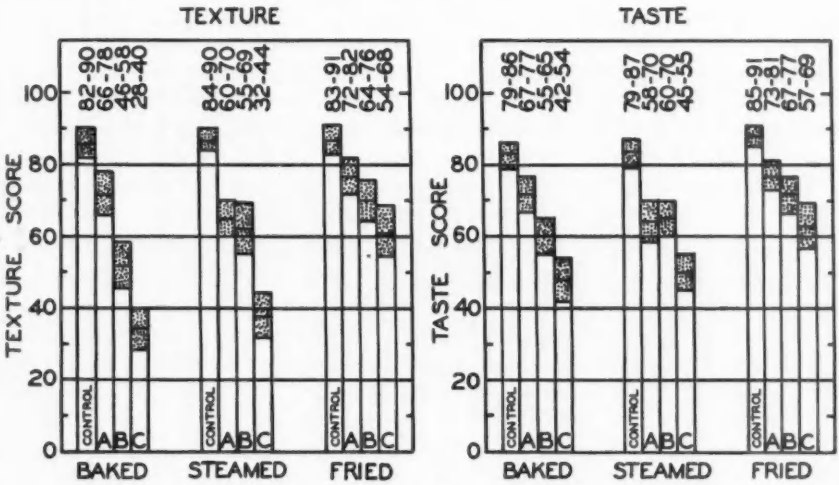

Fig. 3. Comparison of baking, steaming and frying cooking methods on texture and on taste scores of frozen cod fillets of good (A), medium (B) and poor (C) frozen storage qualities. Average scores are shown, with 95% confidence limits indicated by the range. For convenience, figures for the range are also given.

With baked and fried samples, the scores of the known control, good (A), intermediate (B), and poor (C) samples decrease in a regular order, whereas in the steamed samples, the good sample (A) is not separated from sample B.

Many tasters did not like the steamed samples as well as the baked or fried ones, although some remarked that odours could be distinguished more readily. This dislike may possibly explain the difference found between the known and unknown steamed controls. Since the former was known to be of good quality,

it was probably scored artificially high even though the individual tasters may not have liked it. However, when the other samples were tasted, there was no such incentive for a high score, and the result was a more realistic evaluation of the acceptability of this sample to the panelists. Whatever the reason may have been for the downgrading of the unknown "good" sample (A), the panelists were unable to distinguish it from the B sample of intermediate quality. It seems unlikely that this could be the result of some variant in the cooking procedure, since all samples tasted at one time were cooked alike; three separate panels were used on different days, and all of the samples were not from the same part of the carton since the various cooking methods were also randomized in sequence. Thus, for the samples used, steaming does not seem to give as uniform results as baking, although there is little difference in standard errors for all three methods

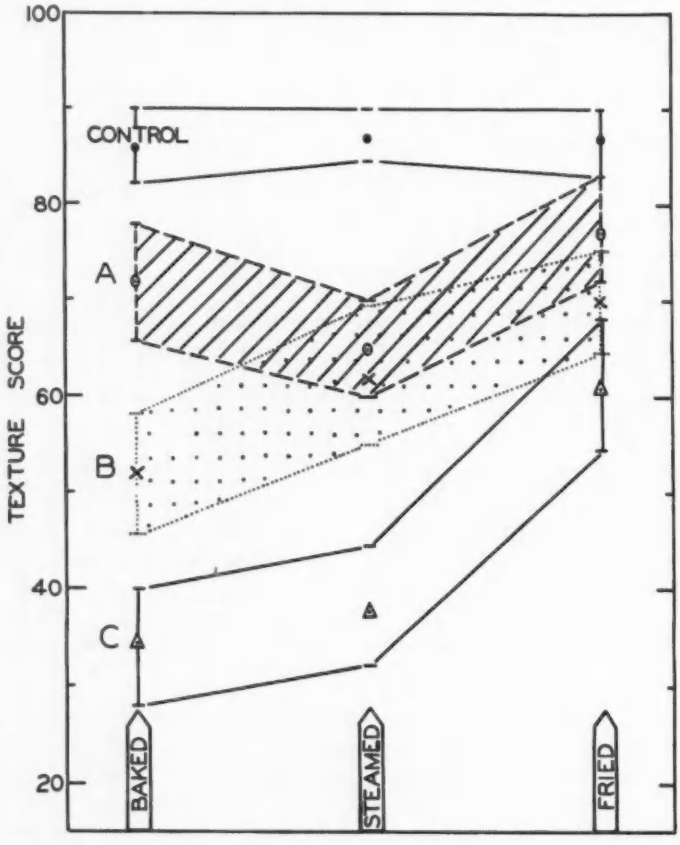

FIG. 4. Ability of cooking method to differentiate between cod fillets of various frozen storage qualities (95% confidence limits are shown).

(Fig. 4). Steaming does not emphasize taste differences in preference to texture (Fig. 3); in fact, the texture scores run comparatively lower than taste scores with decreasing frozen storage quality. Though no data are presented, better discrimination of flavour changes has been given as one of the reasons favouring steaming over baking procedures in assessing quality in iced fish (Shewan *et al.*, 1953). However, our results show that this conclusion does not seem to be valid in the case of frozen storage quality deterioration.

That frying is an effective means of masking adverse flavour and texture change is supported with a few scattered observations in the literature, e.g. in deep-frying of oysters (Morton and Dyer, 1956), cod subjected to irradiation pasteurization (Carver and Steinberg, 1959), the flavour and aroma of freshwater fish from various sources (Baldwin *et al.*, 1962).

Significance to Taste Panel Testing and to Consumer Acceptance

The results of the present study show that three standard cooking methods produced varying palatability scores with frozen cod fillets in different stages of frozen storage deterioration. With an analytical taste panel and a scoring procedure designed to characterize and measure differences in texture, flavour, odour, and other characteristics resulting from initial bacterial spoilage or from frozen storage deterioration, baking appears to be the most discriminatory method of cooking. Steaming is less effective in distinguishing very good from medium quality fish, while frying largely obscures the characteristic frozen storage quality changes. With neither cooking method did the tasters distinguish between the various degrees of initial freshness in the samples used.

If, however, the object of testing is to gauge the palatability of the product in terms of consumer acceptance (for a discussion of taste panel aims and interpretation see Jellinek, 1962), then the assessment must be related to the method of preparation used. If, for instance, most consumers fry the product, then the recommendation for frying should be based on testing by this method. At the same time, of course, the results by the more sensitive baking procedure will indicate whether the product is losing its top quality, and even though still acceptable when fried, the product may have lost much of its taste appeal. It will also be evident that the quality of the product available will determine which method the cook should use to get the most from it.

Consideration of texture and taste scores (Fig. 3) indicates that the best quality frozen fillets may be either baked, steamed, or fried, all methods being capable of bringing out the full flavour of the fish and resulting in high palatability levels. In such a case the consumer has a choice of cooking methods for variety. For fish of poor or doubtful quality, on the other hand, frying is the consumer's best choice of preparation, since palatability is considerably increased by the resultant masking of quality defects. Since at the present time, some frozen fish reaching the retail market is unfortunately not of top quality, a method of cooking selected to produce maximum palatability with the product at hand is worthy of the housewife's careful consideration.

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Retinomotor Cycles and Correlated Behavior in the Teleost *Astyanax mexicanus* (Fillipi)[1,2]

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ABSTRACT

Dark-adapted *Astyanax* exposed to light at 5 ft-c schooled in about 15 sec during the day, but only after a lapse of about 6 min at night. This behavioral rhythm was closely synchronized with the natural diel cycle and was correlated with a retinomotor rhythm. At night the retina was histologically dark-adapted. During the day it was in an intermediate condition with the rods and cones, on the average, near their light-adapted positions. The pigment was in part concentrated near the basal cell layer as in the dark-adapted retina. The remainder was extended as in the light-adapted retina but did not form a dense light-occluding band proximal to the rod ellipsoids.

INTRODUCTION

In the course of observations on the schooling behavior of *Astyanax mexicanus*, the black-banded tetra, we noted that the schooling response of dark-adapted fish varied synchronously with the natural diel cycle. Upon sudden exposure to light at about 5 ft-c, during the day, the fish schooled in about 15 sec. At night they continued swimming randomly as they do in darkness, though with greater vigor, for about 6 min before forming a school.

Kawamoto and Konishi (1955) reported that dark-adapted *Girella punctata* Gray and *Rudarius ercodes* Jordan and Fowler exhibited a diel rhythmic phototaxis in response to illumination. Although they mentioned possible underlying mechanisms that might explain this rhythm, they did not discuss retinomotor activities. Retinomotor rhythms in continuous darkness were described for *Amieurus* (Welsh and Osborn, 1937; Arey and Mundt, 1941) and for *Carassius auratus* (Wigger, 1941), but the accompanying behavior of these fishes was not discussed. In some fishes, for example juvenile *Oncorhynchus* (Ali, 1959), there is no persistent retinomotor rhythm. However, all investigations have shown that in continuous light the eyes remain consistently light-adapted.

As a first step toward understanding the behavior of *Astyanax* we have made histological preparations of the eyes to learn whether there is a persistent retinomotor rhythm in darkness.

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BEHAVIORAL RHYTHM

Observations on the responses of dark-adapted *Astyanax* to sudden illumination at 5 ft-c were not pursued exhaustively because the bright light disrupted the routine of the schooling experiments, but the data that were obtained define the behavioral rhythm sufficiently for present purposes.

The results are based on five different groups of six to nine adult fish. One group was conditioned to an artificial diel cycle; the others were conditioned to the natural cycle. In the collective experiments, the fish were placed in darkness at every hour from 0800 to 2400. They were observed after different durations of darkness varying from 2 to 48 hr. In one experiment the fish were confined to darkness for 96 hr and were observed twice in each 24-hr period. In one other experiment the fish were exposed to the light, only long enough for the observation, at 3-hr intervals beginning with 1940 hr.

The end-point in each observation was the time at which all fish joined the school. This varied with groups and between groups but the variations did not obscure the basic behavioral rhythm. Within the limits of these experiments, it made no difference when the fish were placed in darkness or how much time lapsed before the observation was made provided that the fish had sufficient time to become dark-adapted. During the day they always schooled within a few seconds and at night only after a longer delay. The rhythm persisted for 96 hr in spite of the two disruptions in each 24-hr period. We do not know how long it might persist but would expect it to fail within a few days as is generally the result with circadian rhythms. Exposure to light at 3-hr intervals destroyed the rhythm after 36 hr. Thereafter, the fish behaved the same as dark-adapted fish during the day. The fish under the artificial diel cycle schooled in 15–25 sec after the light came on in the morning. (These morning observations from the artificial cycle are not included in Fig. 1.)

The behavioral cycle is generalized in Fig. 1 with a curve fitted by eye. The observational times for various days were normalized relative to sunrise and sunset. Where observational points are lacking or are too few in number, the form of the curve is suggested by the broken line.

Clearly, the transformation of behavior is abrupt and closely synchronized with sunrise and sunset. At 18 min before sunrise the schooling time was 4 min 40 sec. It fell to the minimum at the instant of sunrise. At the instant of sunset, the schooling time was 2 min 50 sec, and within 15 min after sunset was near the maximal value. The cycle appears to consist of two plateaus connected by sharply inclined transitional slopes. The diurnal plateau seems adequately defined. However, owing to insufficient observations, it would be presumptuous to conclude at this stage that the nocturnal phase is definitely a smooth plateau. In a detailed study of the duration of the light-shock reaction of *Lepomis* at night, Davis (1962) found, after the fish were adapted to the artificial cycle, a rapid rise in time reaching a maximum about 4 hr after darkness. During the remaining 8 hr, the time fell continuously reaching a value of about one-third of maximum just before sunrise. Yet, the long delay before schooling

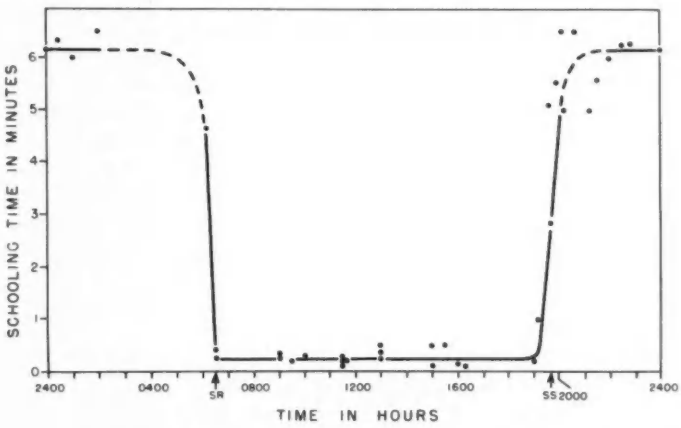

FIG. 1. The cyclic behavior of *Astyanax* in continuous darkness as revealed by the time-lapse between the application of light and the formation of a school. Each point represents one test. SR = sunrise, SS = sunset. See text for further description.

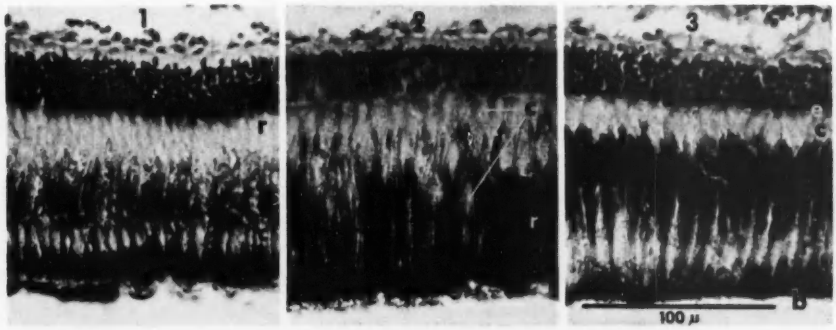

FIG. 2. Photomicrographs of visual cell layers of retinas: (1) midnight-darkness, (2) noon-darkness, (3) noon-light; b = basal pigment cells, c = cones, e = external limiting membrane, r = rods. Cones can be readily identified by their large ellipsoids but the rods are inconspicuous in the photomicrographs and only their general location can be indicated. Fixed with Harris haematoxylin and eosin.

shown by *Astyanax* at 18 min before sunrise indicates that if there is a decline through the terminal hours of darkness, it proceeds at a much lower rate than in *Lepomis*.

The behavioral rhythm not only was synchronized with the diel cycle but also it was regulated by light as shown by the results under the artificial diel cycle. We do not know the critical intensities of illumination that initiated the behavioral changes, but whatever they are it appears that the internal response mechanisms in the fish include an anticipatory component which is itself directly regulated by the light, and secondarily modifies the total mechanism so that the transition in behavior precedes the condition to which it is directed. *Astyanax* adapted to the artificial abrupt changes in illumination without the complications of morning and evening gradients of light, which could serve as stimuli, schooled within the minimum time (15–25 sec) at the instant the light came on. This indicates that the transition in behavior was completed before the occurrence of the stimulus.

RETINAL RHYTHM

Two fish were used in each treatment. To obtain dark-adaptation at noon, the fish were placed in the darkroom at 2200 hr, having been in near darkness for 5 hr from sunset, and fixed at 1200 hr the following day. Fish light-adapted in a room illuminated by both natural and artificial light were fixed at 1200 hr. For dark-adaptation at midnight, the fish were placed in the darkroom at sunset and fixed at 2400 hr. For light-adaptation at night, the fish were fixed at 2400 hr, having been exposed to artificial illumination continuously from 0800 hr. The temperature was 25±1°C.

The fish were fixed in 10% formalin, the dark-adapted fish being fixed in darkness. The corneas and lenses were removed after 12 hr, and after 24–36 hr, the eyes were extracted, dehydrated through an ethyl alcohol series and embedded in paraffin. Sections were cut at 10 μ and stained with Harris haematoxylin and eosin.

The positions of the visual cells relative to the external limiting membrane were measured with an ocular micrometer. Twenty-five measurements of adjacent elements were made from a particular area of each retina of one eye from one fish of each treatment. In using only one eye, we are not suggesting that the eyes within a species show no variations. However, we found that the eyes from both fish in each treatment were in the same general histological state.

Photomicrographs (Fig. 2) show the marked histological differences in the midnight dark-adapted, noon dark-adapted, and noon light-adapted retinas. The midnight light-adapted retina could not be distinguished from the noon light-adapted retina. The midnight dark-adapted and noon light-adapted retinas illustrate the classical extreme shift in the positions of rods, cones, and pigment.

The bulk of the pigment in the light-adapted retina lay in a dense band between the rod and cone ellipsoids and presumably shielded the rods from

incident light. In the midnight dark-adapted retina, the pigment was concentrated near the basal cell layer and though some of it was dispersed toward the external limiting membrane, it lay distal to the rods.

In the noon dark-adapted retina, the components illustrated a distribution intermediate between dark- and light-adaptation, very suggestive of the condition of the retina of *Pterophyllum eimeckei* in dim light, illustrated by Braemer (1957). The cone ellipsoids lay predominantly against the external limiting membrane but some occurred within the pigment as much as half the distance between the external limiting membrane and the basal cell layer. The rod myoids were extended in the noon dark-adapted eye, but not as much as in the light-adapted eye. Thus, the rods and cones were in general near their positions of light-adaptation. The pigment in the noon dark-adapted eye was in part concentrated near the basal cell layer with the remainder extended in discrete processes toward the external limiting membrane. Some of the processes were extended as much as in the light-adapted eye. Relative locations of the visual cells are given in Table I.

TABLE I. Mean values with standard deviations of 25 measurements of the positions of rods and cones in retinas at midnight-darkness, noon-darkness, and noon-light. The values represent the distances from the external limiting membrane to (1) the priximal margin of the rod ellipsoid and (2) the proximal margin of the cone ellipsoid, each expressed as a percentage of the distance from the external limiting membrane to the basal pigment cell layer. In the midnight-dark-adapted eye, the contraction of the myoids draws the ellipsoids of the rods beyond the external limiting membrane.

Condition of retina	Relative distance from external limiting membrane	
	To rod ellipsoid	To cone ellipsoid
	%	%
Midnight-dark-adapted	$-1 \pm .03$	$53 \pm .06$
Noon-dark-adapted	$18 \pm .02$	$20 \pm .03$
Noon-light-adapted	$45 \pm .08$	$2 \pm .02$

DISCUSSION

Because schooling in *Astyanax* as in other fishes is dependent upon vision, the time-lapse of 6 min from the instant of illumination to formation of a school at night would appear to represent the necessary time for the adjustment of the retina from scotopic to photopic conditions. This visual adjustment would include the bleaching of visual pigments as well as some shift in retinal elements. However, because behavior may be the manifestation of multiple conditions, one cannot unequivocally conclude from these experiments that the time-lapse to schooling is a simple uncomplicated measure of the rate of visual adjustments. The perfection of photopic vision adequate for schooling could precede the act of schooling by some fraction of the total lapsed time. These non-visual components might account for some of the variation in the time-lapse before schooling.

On the other hand, the fact that the fish had adequate vision for schooling need not mean that the retinal elements had reached the positions of maximum adaptation in the 6-min interval. Ali (1959) found that dark-adapted *Oncorhynchus* schooled before their retinas had assumed the maximum state of light-adaptation.

From the limited data on *Astyanax*, one cannot conclude that the behavioral and retinomotor rhythms are precisely synchronized. It would appear, however, that the retinomotor cycle is primary and that in its determination of the visual ability it regulates the behavioral cycle. This interpretation is consistent with the statement of Walls (1942) that teleost fishes in general are unable to traverse habitats with pronounced light gradients because they cannot make rapid visual adjustments.

The retina of *Astyanax* in continuous darkness seems to behave like that of *Carassius* (Wigger, 1941), in which the rhythm involves shifts in both the visual cells and the pigment and leads to an intermediate condition of the retinal elements in darkness at noon. Studies of retinomotor rhythms have been made on only a few species of fishes and the varying results obtained at this stage fail to point clearly to any particular generalization. The retina of *Amieurus* (Welsh and Osborn, 1937; Arey and Mundt, 1941) in continuous darkness exhibits a rhythmic shift in the visual cells but not in the pigment, and juvenile *Oncorhynchus* (Ali, 1959) show no persistent retinomotor rhythm.

The ultimate question is the biological significance of the persistent retinomotor rhythm. The occurrence of the rhythm in continuous darkness is an interesting experimental phenomenon but not necessarily a meaningful biological phenomenon because for these fishes darkness throughout the daytime hours is an abnormal condition. The behavioral shift preceding sunrise could have biological significance insofar as it implies a retinal adjustment which would equip the fish with good vision throughout the period of relatively rapid transition from darkness to full sunlight. The behavioral shift preceding sunset indicates the reverse process, that the eye is preparing for continuity of vision in the forthcoming decline of light.

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Fecundity of the American Plaice, *Hippoglossoides platessoides* (Fabr.) from Grand Bank and Newfoundland Areas[1]

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ABSTRACT

Fecundity estimates were made on a total of 140 mature American plaice from the southern and northern slopes of the Grand Bank and from St. Mary's Bay. Log–log relationships were established between fecundity and fish length, gutted and gilled weight, age, and ovary weight. No differences were found to exist between the fecundity–length relationship of plaice from the three areas, but there is a suggestion that within areas there may be annual differences in egg production. At comparable ages plaice from the southern slope of the Grand Bank are larger in size and produce more eggs than those from the northern slope and St. Mary's Bay.

INTRODUCTION

According to Norman (1934) the species *Hippoglossoides platessoides* (Fabricius) can be divided into two forms, each with its own geographic range. These he regards as two subspecies; the small European subspecies, *Hippoglossoides platessoides limandoides* (Bloch), and the larger North American subspecies, *Hippoglossoides platessoides platessoides* (Fabricius). Between these two in the Iceland and the Barents Sea areas there seems to be an intermediate form which grows to a size between that of the western European and North American forms. In Europe the subspecies is commonly known as the long rough dab whereas the North American subspecies is known as the American plaice, dab, or flounder.

All the previous work on the fecundity of this species was with western European specimens. This form rarely grows beyond 30 cm, and according to Bagenal (1955), in the Clyde Sea area at least, no specimens have been found to be more than 6 years old. Fulton (1891) and Mitchell (1913) give egg counts of 9 and 11 fish, respectively, from the British coast. Bagenal (1957a) gives fecundity estimates for 119 mature fish from the Clyde population. Huntsman (1918), and Bigelow and Schroeder (1953), in brief references to egg production, refer only to the eggs produced by the European subspecies as recorded by Fulton (1891).

The value of fecundity studies has sometimes been questioned and Russell (1942) states that there is no necessary connection between the number of eggs produced in a single year and the number of fry that survive, but rather it is the survival of the eggs and larvae that determines the year-class strength.

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However, fecundity estimates may have some value in population estimations. Buchanan-Wollaston (1926) attempted to estimate the total number of spawning plaice in the North Sea from the abundance of eggs from planktonic sampling and Walford (1938) made a similar estimate with Georges Bank haddock. Simpson (1951), MacGregor (1957), and Nagasaki (1958), were all interested in fecundity studies for such population estimates.

Other possible interests in fecundity are from taxonomic and racial points of view. In the present study a comparison of fecundity at comparable ages shows clear differences between the northern and southern slopes of the Grand Bank.

MATERIAL AND METHODS

Ovaries for fecundity estimates were collected from specimens caught in the three areas shown in Fig. 1. Details of the sampling time, etc., are given in Table I. Some of the ovaries were collected and preserved at sea in which case weights of fish and gonad weights were not recorded; the remainder were collected from specimens examined at the Fisheries Research Board of Canada Biological Station, St. John's, Nfld.

TABLE I. List of samples from which fecundities were estimated.

Area	Date	Number
St. Mary's Bay	Feb. 26, 1957	18
St. Mary's Bay	Apr. 23, 1958	10
N. Grand Bank	Apr. 3, 1958	19
N. Grand Bank	Apr. 29, 1958	13
S. Grand Bank	Feb. 26, 1958	29
S. Grand Bank	Mar. 7, 1961	14
S. Grand Bank	Feb. 11, 1962	37
	Total:	140

The fish lengths are total lengths to the nearest centimetre. Fish are gutted and gilled (i.e. with gills, the alimentary canal and associated organs and the gonads removed), and weighed to the nearest ounce; the weight is then converted to grams. Ovary weights were recorded to the nearest gram.

COLLECTION AND PRESERVATION OF OVARIES

All the ovaries were collected before any of the eggs were translucent, approximately 1 to 2 months prior to spawning. At this stage there is no possibility of counting eggs that will mature the following year since the average diameter of maturing eggs of the present year is approximately 0.8 mm whereas the next generation are less than 0.3 mm.

The ovaries were placed in jars containing Gilson's fluid (as modified by Simpson (1951)) which facilitated the breaking down of ovarian tissue. The

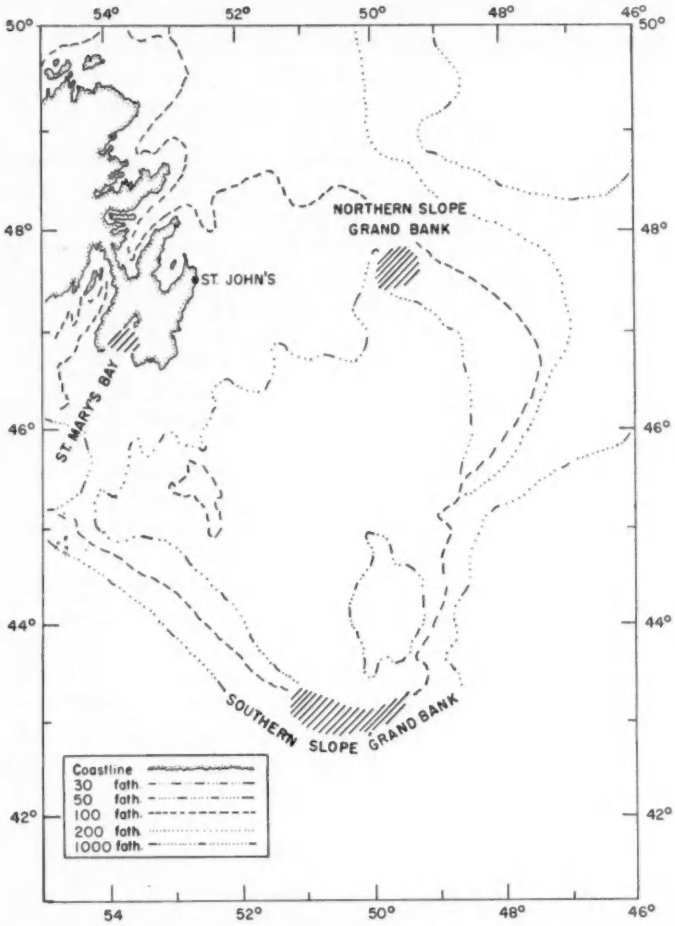

FIG. 1. Areas from which samples were taken for fecundity estimates of American plaice.

ovaries were allowed to remain in this solution for periods of from 3 to 6 months. The 3-month period was found to be the best for cleaning the eggs since for greater periods the outer ovarian wall became soft and could not be peeled away.

In removing the ovarian tissue from the eggs the following method was found to be very satisfactory. The ovaries were placed on fine bolting silk stretched over a large funnel and were broken apart so that parts of the tougher outer walls could be removed with forceps. The remainder of the cleaning was accomplished using a gentle stream of water. After the connective tissue had been satisfactorily washed from the eggs the latter were put into a solution of 10% formalin and stored until counting.

SUB-SAMPLING

Sub-sampling was accomplished by means of a whirling vessel, an apparatus originally designed by E. Lea and G. Rollefsen of the Fisheries Directorate, Bergen, Norway, as a means of sub-sampling plankton samples. Its structure and operation are described in detail by Wiborg (1951).

In the present investigation the method of sub-sampling the eggs was to fill the vessel with water to about 1–1½ inches from the top, pour in the eggs, rotate the vessel quickly before settling occurred and then stop it suddenly. For at least half of the sub-sampling the vessel was rotated by a second operator during the addition of the eggs. After the samples had settled there was no further rotation of the vessel. The usual sub-sample was $\frac{1}{1000}$ of the total, but occasionally $\frac{1}{500}$ was taken. These sub-samples usually consisted of between 750 and 1500 eggs. The procedure was to take 2 samples of $\frac{1}{10}$ of the total, and from each of these again to take 2 samples of $\frac{1}{10}$ to give 4 samples each representing $\frac{1}{100}$ of the total. These were again put through to give 8 samples of $\frac{1}{1000}$ each. Sometimes 2 corresponding $\frac{1}{100}$ samples were combined to give a further fractionation: 4 sub-samples of $\frac{1}{500}$ each. Sometimes only 1 sub-sampling was taken from each $\frac{1}{100}$ fraction to give a total of 4 sub-samples for counting. In all cases 4 or 8 sub-samples were counted and the fecundity was estimated as the average of all the sub-samples for any particular specimen.

In order to test the efficiency of the whirling vessel 2 tests were performed.

TEST A. The results of a test using the whirling vessel in the usual manner, i.e. rotating the vessel before the eggs settled, are given in Table II. An actual count of the eggs at the beginning of the experiment gave a total of 7086 eggs, thus an average of 708.6 for each compartment. After the vessel was rotated in the usual manner, the eggs in 2 of the 10 compartments were counted. The eggs from the remaining compartments were then removed before the next operation. This was repeated 8 times to give 16 sub-samples. The mean number per sampling compartment was found to be 712.8. This is in very close agreement with the actual numbers present even after allowing for the possible loss of eggs and errors in counting.

TEST B. A second test of the equipment was conducted by sub-sampling the eggs from a pair of ovaries in the usual way to obtain sub-samples of $\frac{1}{1000}$. After counting, the sub-samples were added to the remainder and the process repeated 3 times to give 3 sets of estimates of 8 sub-samples of $\frac{1}{1000}$ of the total number of eggs present. All the eggs were removed from the vessel before a new series was started. The object of this was to see if any error was introduced by the use of large numbers of eggs as compared to the comparatively small numbers used in the previous test and, indeed, in Wiborg's (1951) own test of the whirling vessel. It will be noted in Table II that the means of each of the 3 series, 414.1, 411.6 and 408.3, fall within one standard error of the general mean, 411.3, and also that all the individual counts fall within ± 2 standard deviations of the general mean. From this, one may conclude that the sampling mechanics are essentially accurate and give a true indication of the actual numbers present.

TABLE II. Egg counts from two tests of the efficiency of the whirling vessel.

A	B	
Vessel rotated before eggs settled	Usual procedure with large number of eggs	
736	*Series I*	
674	1	2
669	378	482
633	432	384
820	449	353
720	485	350
686	Mean 414.1	
601		
605	*Series II*	
690	1	2
735	439	430
756	431	385
738	446	380
806	382	400
723	Mean 411.6	
812		
	Series III	
	1	2
	382	380
	325	376
	487	451
	450	415
	Mean 408.3	
$N = 16$	$N = 24$	
$\overline{X} = 712.8$	$\overline{X} = 411.3$	
$S_x = 67.5$	$S_x = 44.9$	
$S_{\bar{x}} = 16.9$	$S_{\bar{x}} = 9.2$	
Actual number in sample 7086		

FECUNDITY RELATIONSHIPS

The fecundity of this species has been related to length, weight, age, and ovary weight. In all cases it was found that a double logarithmic transformation gave linear relationships. Logarithms to the base 10 taken to 3 places of decimals were used in all cases and the fecundity expressed in thousands of ova.

Table III gives the constants for the various fecundity relationships together with the coefficients of correlation for each of these. Statistical comparisons using analysis of covariance are by the methods given by Snedecor (1956).

RELATION BETWEEN FECUNDITY AND FISH LENGTH

Figure 2 is a scatter diagram of fecundity plotted against the length of fish. Using the data from all samples, fecundity was found to increase with length to the following relationship:

$$F = 0.002103L^{3.1709}$$

(where F = fecundity in thousands of ova, and L = length in centimetres). The coefficient of correlation (r) for this relationship is highly significant (Table III).

TABLE III. Summary of the intercepts, regression coefficients and correlation coefficients of the various fecundity relationships.

Log fecundity in relation to	Intercept (a)	Regression coefficient (b)	Correlation coefficient (r)	Test of statistical significance
Log length (all areas)	−2.6772	3.1709	0.874	P = <0.001
Log (gutted and gilled) weight (all areas)	0.0380	0.9011	0.872	P = <0.001
Gutted[a] and gilled weight (all data)	73.59	0.453	0.810	P = <0.001
Log ovary weight	1.2735	0.6848	0.750	P = <0.001
Log age (all areas)	1.3367	1.1781	0.478	P = <0.001
Log age (northern area)	1.4228	0.9599	0.473	P = <0.01
Log age (southern area)	1.5050	1.1403	0.705	P = <0.001

[a]Fecundity against weight.

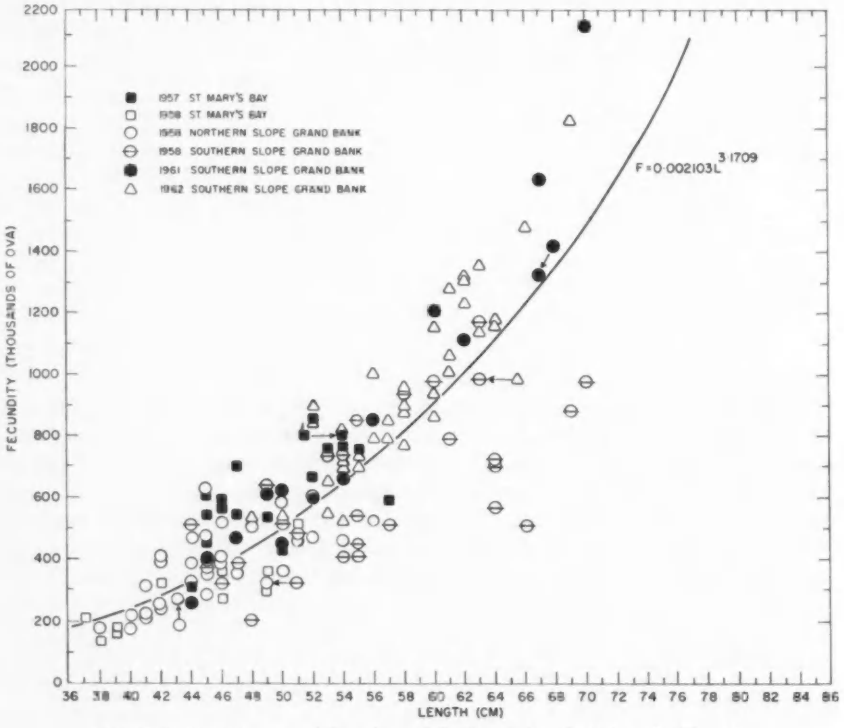

FIG. 2. Scatter diagram of American plaice fecundity plotted against length.

COMPARISON OF AREAS. For the three areas from which the samples were taken the following equations have been calculated (F being in thousands of ova in all cases):

(i) St. Mary's Bay. Log F = 3.7944 Log L − 3.7090 (28 specimens)
(ii) Northern slope of the Grand Bank. Log F = 2.6773 Log L − 1.8602 (32 specimens)
(iii) Southern slope of the Grand Bank. Log F = 3.0382 Log L − 2.4445 (80 specimens)

An analysis of covariance indicates that there is no significant difference either between the slopes (F = 1.60 for F_{05} = 3.07) or adjusted means of log fecundity plotted against log length for these three areas (F = 0.63 for F_{05} = 3.07), in spite of the fact that, as we shall see later, plaice from the southern slope of the Grand Bank are larger at comparable ages and mature at larger sizes than those of the other two areas (Fig. 5).

Comparing samples for the same year (1958) from the northern and southern slopes of the Grand Bank also indicates no significant differences between slopes (rate of fecundity increase) (F = 1.25 for F_{05} = 4.07) or adjusted means (F = 0.50 for F_{05} = 4.07).

COMPARISON OF YEARS. A comparison was made between the fecundity–length relationships of the samples for 4 different years. The rates of fecundity

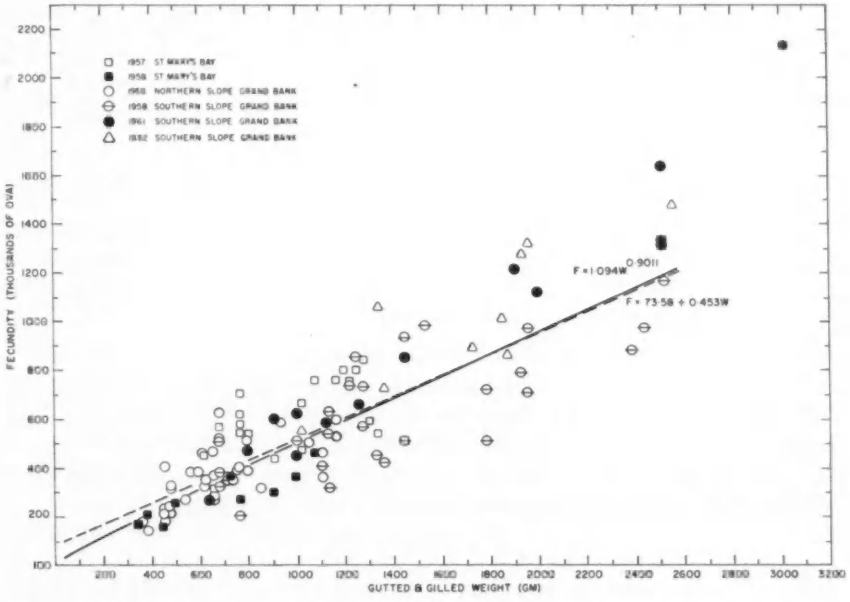
1957 ST MARY'S BAY
1958 ST MARY'S BAY
1958 NORTHERN SLOPE GRAND BANK
1958 SOUTHERN SLOPE GRAND BANK
1961 SOUTHERN SLOPE GRAND BANK
1962 SOUTHERN SLOPE GRAND BANK
F = 1.094W^0.9011
F = 73.58 + 0.453W
FECUNDITY (THOUSANDS OF OVA)
GUTTED & GILLED WEIGHT (GM)

FIG. 3. Scatter diagram of American plaice fecundity plotted against gutted and gilled weight.

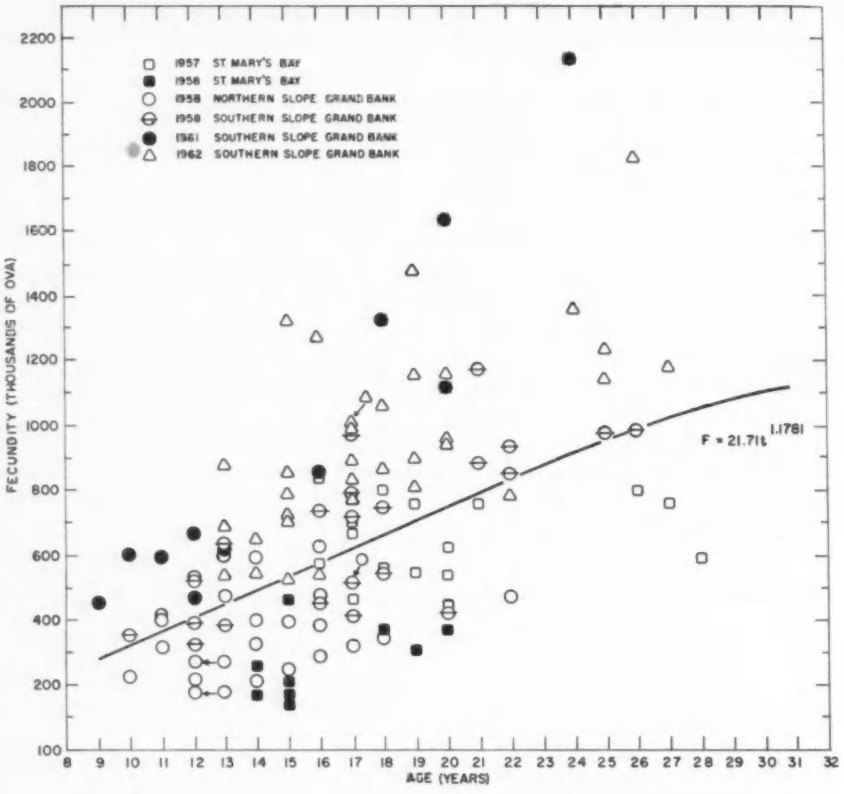

FIG. 4. Scatter diagram of American plaice fecundity plotted against age.

increase are significantly different at the 5%, but not at the 1% level ($F = 4.09$ for $F_{05} = 2.84$ and $F_{01} = 4.31$). This suggests the possibility of differences in the number of eggs produced in different seasons. However, some of the samples are comparatively small, e.g. 18 for 1957 and 14 for 1961.

RELATION BETWEEN FECUNDITY AND FISH WEIGHT

For most of the specimens taken, the gutted and gilled weight was recorded. The only exceptions to this were the samples taken at sea. The number of eggs at various fish weights (gutted and gilled) is illustrated in Fig. 3.

Log fecundity plotted against log weight (in grams) gives the relationship as shown in the following equation (Table III):

$$F = 1.094W^{0.9011}$$

(where F = fecundity in thousands of ova, and W = gutted and gilled weight in grams).

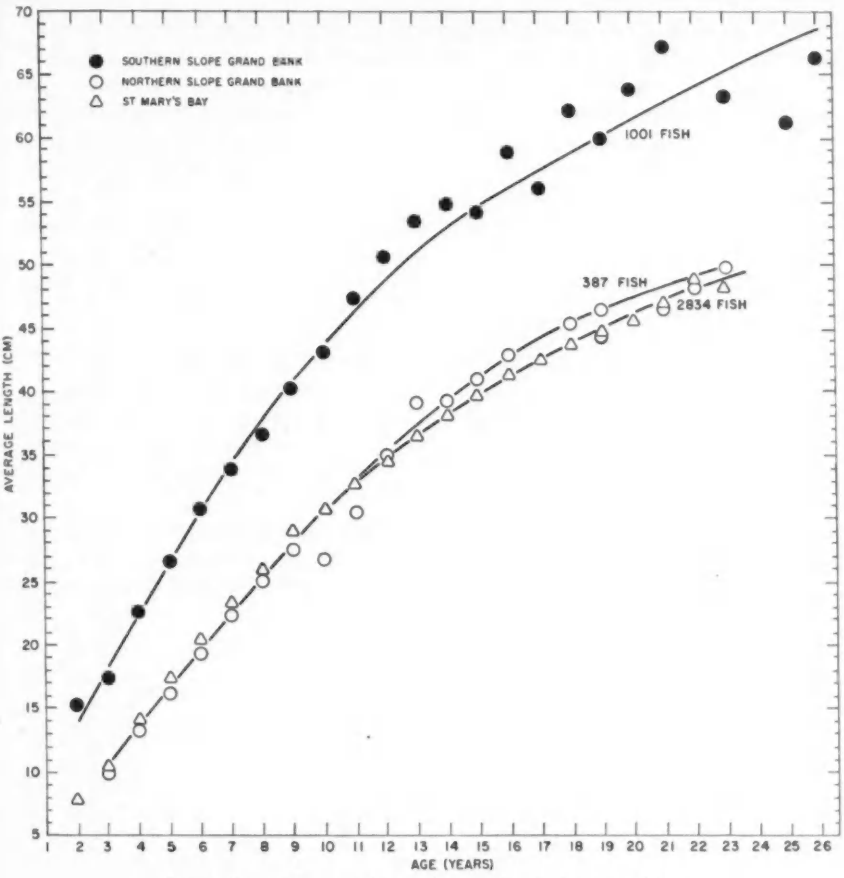

FIG. 5. Growth curves of American plaice for three localities.

Fecundity plotted against gutted and gilled weight gives the following (Table III):

$$F = 73.59 + 0.453W$$

The linear relationship is to be expected since the relationship of gutted weight to length is $W = 0.0078L^{3.0370}$ (unpublished data of the Fisheries Research Board of Canada Biological Station, St. John's) which is similar to that found for fecundity against length ($F = 0.002103L^{3.1709}$).

RELATION BETWEEN FECUNDITY AND AGE

Figure 4 gives the fecundity of individual plaice plotted against age as a scatter diagram. The great range in fecundity for the various ages can be observed from this diagram. The equation for the relationship between fecundity and age using all the data for all three areas is as follows:

$$F = 21.71t^{1.1781}$$

(where F = fecundity in thousands of ova, and t = age in years). However, the combined data do not give a correct picture of the relationship.

Figure 5 gives growth curves for the three areas under consideration. Plaice samples from the northern slope of the Grand Bank and St. Mary's Bay have practically identical growth curves and thus for the purpose of examining fecundity–age relationships these two areas can be combined. This increases the number of observations for a single northern area.

Using all the samples, fecundity was found to increase with age for the two areas as follows (Table III):

$$\text{(i) Northern Area Log } F = 1.4228 + 0.9599 \text{ Log } t$$

$$\text{(ii) Southern Area Log } F = 1.5050 + 1.1403 \text{ Log } t$$

(where F is fecundity in thousands of ova, and t the fish age in years). The coefficients of correlation (r) for (i) and (ii) are statistically significant (Table III).

Figure 6 shows the above relationship. The rate of increase in fecundity with respect to age is not significantly different for the two areas compared ($F = 0.43$ for $F_{05} = 3.95$), however, the average fecundity adjusted to a common age is significantly different statistically ($F = 99.03$ for $F_{05} = 3.94$).

Using the average log fecundity (geometric) at each age gives a correlation coefficient (r) for the northern areas of 0.084 and for the southern 0.940. Both are highly significant. The equations for the log average fecundity with respect to log age are as follows:

$$\text{Northern Area Log } F = 1.7134 + 0.97380 \text{ Log } t$$

$$\text{Southern Area Log } F = 1.3349 + 1.0629 \text{ Log } t$$

(where F = average fecundity in thousands of ova, and t = age in years).

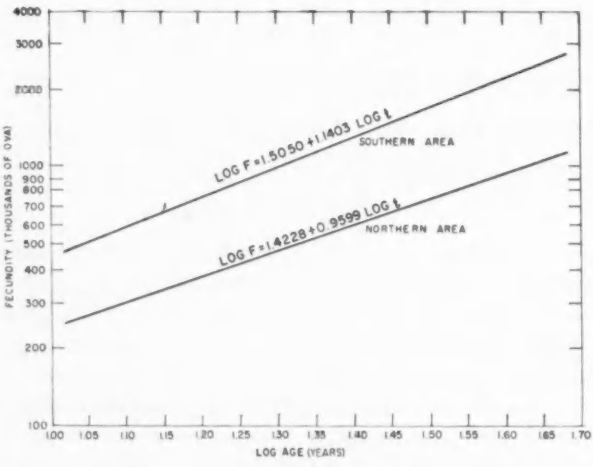

FIG. 6. Weighted log–log regression lines of American plaice fecundity on age for southern area (southern slope of the Grand Bank) and northern area (northern slope of the Grand Bank and St. Mary's Bay).

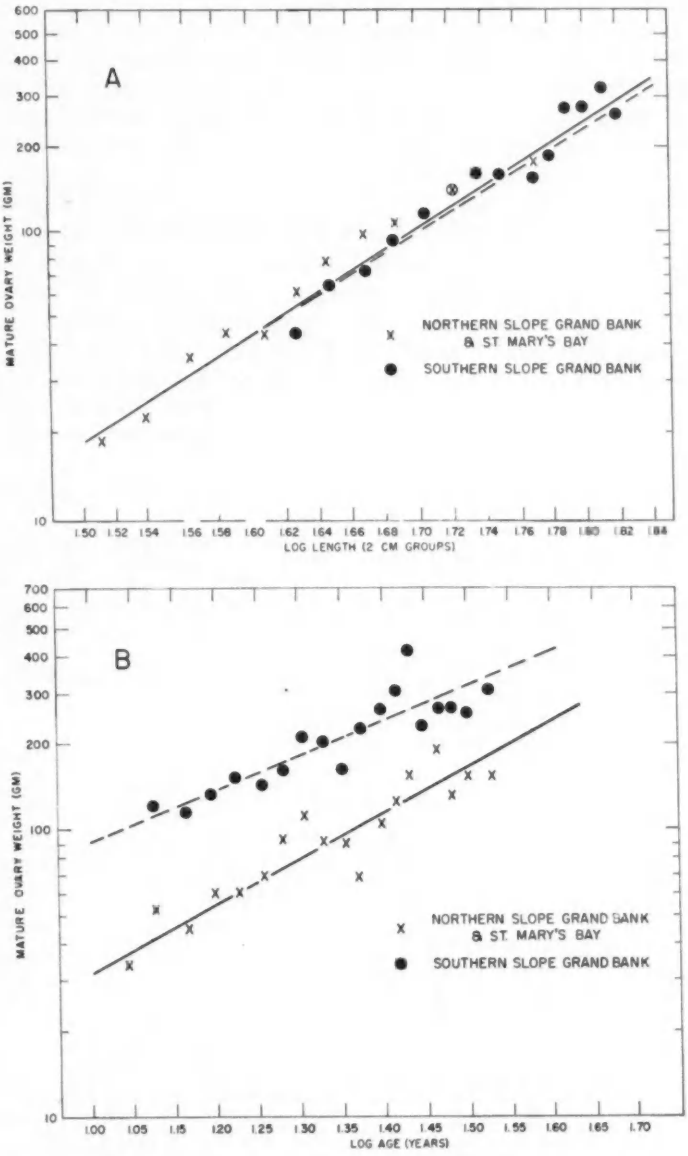

FIG. 7. A. Mature ovary weight against length; B. mature ovary weight against age.

The reason why plaice from the southern area produce more eggs at comparable ages than those of the northern area can be explained by the differences in the size of this species of the same ages from these two areas. As we have seen there is no significant difference between the number of eggs produced by plaice from the two areas at comparable body length. However, at any given age, plaice from the southern slope of the Grand Bank will be considerably larger than those from the two more northerly areas and will therefore produce more eggs.

Figure 7A gives the log ovary weight (geometric average) of mature fish plotted against log body length. The rate of increase in ovary weight with

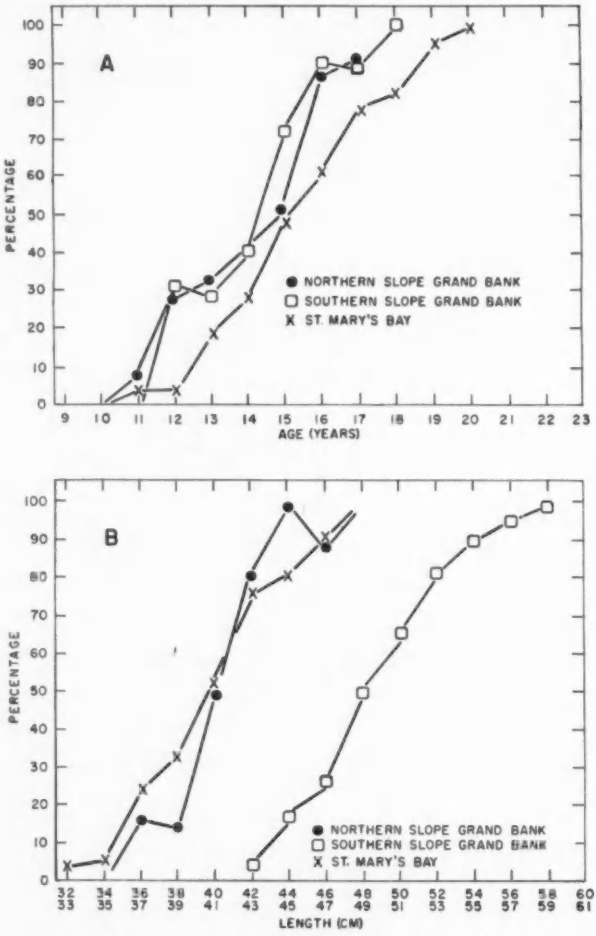

FIG. 8. Percentage of American plaice mature at various ages (A) and lengths (B).

respect to body length is practically identical for both areas. However, from a glance at the points plotted on this Figure it can be seen that all the observations from the 30–31 to the 40–41 cm group inclusive are from the northern areas (St. Mary's Bay and northern slope of the Grand Bank) (Log 40 = 1.602).

Figure 7B gives the plot of log mature ovary weight (geometric average) against log age. Here again the rates of increase in ovary weight for the two areas are similar ($F = 2.84$ for $F_{05} = 4.17$ and $F_{01} = 7.56$) but the average ovary weights adjusted to a common age are entirely different ($F = 135.3$ for $F_{05} = 4.15$ and $F_{01} = 7.50$). This shows that at comparable ages the ovaries of fast-growing fish are larger than those of slower-growing stock.

The apparent reason why the faster-growing fish have larger ovaries at first maturity can be seen from Fig. 8, where it is shown that there is very little difference between stocks in the age at which female plaice mature. The 50% mature point for all three areas is between 14 and 15 years and some females for each area are mature at 10–12 years. Compared with this, the per cent mature in relation to length indicates a great difference in size at first maturity for the northern and southern areas with the 50% mature point at 40–41 cm for the two

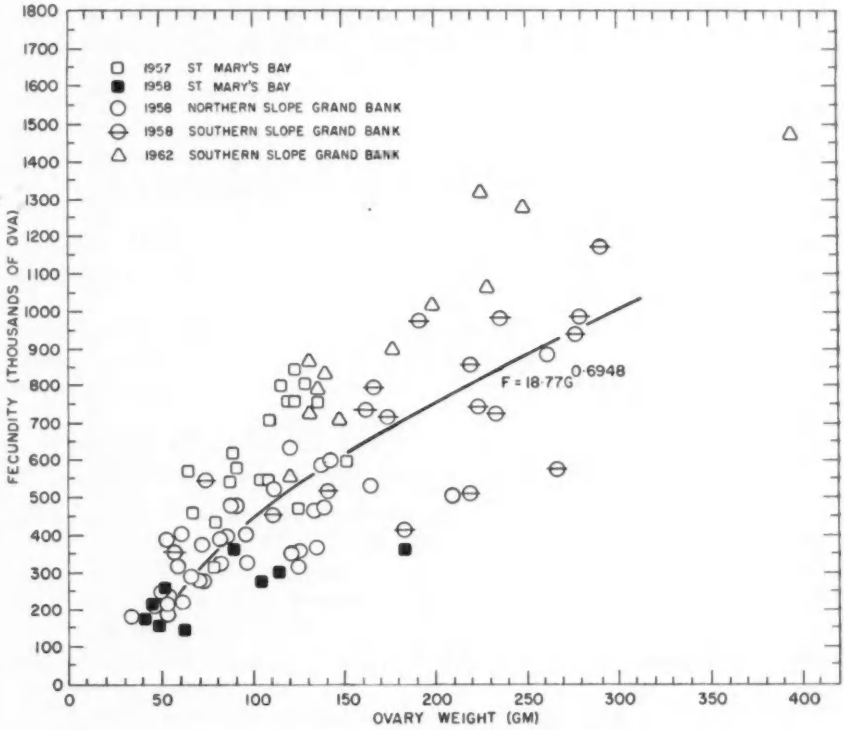

FIG. 9. Scatter diagram of American plaice fecundity plotted against mature ovary weight.

northern localities (St. Mary's Bay and northern slope of the Grand Bank) and at 48–49 cm for the southern slope of the Grand Bank. Ovary size is directly related to fish size, so that plaice from the southern slope of the Grand Bank maturing for the first time have larger ovaries than those from the slow-growing northern stocks. As a result more eggs are produced at comparable ages since as we shall see there is a good relationship between fecundity and ovary weight.

Relation Between Fecundity and Ovary Weights

Figure 9 is a scatter diagram of fecundity plotted against the weight of ovary. The increase in fecundity with respect to the weight of ovary can be expressed as follows:

$$F = 18.77G^{0.6967}$$

(where F = fecundity in thousands of ova, and G = weight of ovary in grams).

The coefficient of correlation (r) is highly significant (Table III).

DISCUSSION AND CONCLUSIONS

Fecundity of 140 samples of American plaice from the northern and southern slopes of the Grand Bank and from St. Mary's Bay was found to be directly related to length, weight, and to a somewhat lesser extent, age of the fish. This is confirmed statistically by the correlation coefficients for the various fecundity relationships which are for the most part all highly significant, indicating good linear relationships (Table III). In the case of log fecundity on log age the correlation coefficient is a little lower, but still significant statistically. However the difficulty in using age arises from the significant difference in the average fecundity adjusted to a common age for the two areas brought about by the fact that plaice from the southern slope of the Grand Bank are up to 10 cm larger (although of approximately the same age) when they mature. Add to this the probability of error in age interpretation and it is apparent that generally speaking the calculation of fecundity from age is rather hazardous.

Table IV compares the rate of egg production (regression coefficients) of the European and North American forms of *Hippoglossoides platessoides*. These figures are remarkably similar, however; it should be noted that the females of

Table IV. Comparison of the regression coefficients for the fecundity relationships of the North American and European forms of *Hippoglossoides platessoides*. (Data for European form from Bagenal, 1957a.)

Log fecundity related to	North American form	European form
Log length (*cm*)	3.1709	3.5533[a] and 3.0621[b]
Log weight (*g*)	0.9011	1.1388[a] and 0.9461[b]
Log age (*years*)	1.1781	1.0033[a] and 1.0328[b]
Log av. wt. (*g*)	0.6848	0.6907[a] and 0.8117[b]

[a]February 1954 samples.
[b]March 1954 samples.

the European form mature at much smaller sizes (down to 15 cm) and at a much younger age (2 years) than the North American form where the smallest mature female specimen was 37 cm and the youngest 9 years.

On the basis of the data available there is no significant difference between the log fecundity–log length relationships for plaice populations that differ in size at comparable ages, so that it would appear that the equation found for this relationship can be used for all the spawning populations of this area. However, this particular aspect perhaps needs further investigation using larger numbers of ovaries from specimens of comparable sizes for the same year. In the northwest Atlantic there appear to be many other areas that support spawning populations and it is hoped that at a future date these will be compared with the areas investigated in this paper.

Bagenal (1957b) reports a statistically significant difference at the 1% level for the fecundity of the European form of this species for the years 1954–1956, and other authors have found yearly fluctuation in the number of eggs present in plankton samples which could possibly be attributed to a varying number of eggs being produced. In the present investigation, because of the smallness of the samples, the evidence of yearly fluctuation in fecundity is not strong enough to make a conclusive statement; one would be led however to suspect that such is the case.

ACKNOWLEDGMENTS

The author is particularly indebted to Mr C. A. Rose for his capable work in making most of the egg counts as well as the preliminary work in collecting the species, preparing the eggs for sampling, and carrying out much of the statistical calculations. Grateful acknowledgment is also extended to the several members of the scientific staff who made many helpful suggestions in the preparation of the manuscript for publication.

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Net Avoidance Behavior of Carp and Other Species of Fish[1]

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ABSTRACT

The net avoidance behavior of carp, *Cyprinis carpio* Linnaeus, was studied in the laboratory. The effect of the size of the tank, temperature, light, social behavior, and air bubbles was evaluated and the behavior of carp was compared to that of nine other species of freshwater fishes.

Carp tended to escape a net in the same relative position in tanks of different lengths. Fish in cold water used a bottom escape route while those in warm water used an escape route located at the top of the net. Groups were more successful in avoiding a net than were isolates. In warm water there was an immediate difference between the performance of groups and isolated fish; in cold water differences appeared after training. Blind carp and carp tested in turbid water were less successful in avoiding a net than were fish with unimpaired vision. Groups of carp avoided portions of an escape route which were occluded by air bubbles.

INTRODUCTION

A laboratory approach to the problem of net avoidance has been utilized by a number of Japanese investigators. The responses of fishes to nets of various colors has been studied by Hiyama *et al.* (1957), Kusaka (1957b), Kanda and Koike (1958a, b), Kanda *et al.* (1958a, b), and Kusaka (1958). Other investigations include the reaction of fish to nets of various mesh sizes (Kusaka, 1957a), the response of fish to bubble nets or air curtains (Sumio, 1960), the behavior of fish after confinement in semi-transparent and opaque containers (Kusaka, 1961), and the responses of fish to nets inclined at several angles (Hiyama *et al.*, 1959).

In the present study, the size of the tank, temperature, light, social behavior, and air bubbles were evaluated for their effect on the responses of fish to a moving net. Juvenile carp, *Cyprinus carpio*, 80–202 mm in total length, were selected as the experimental animal for nearly all experiments owing to the importance of carp control in Wisconsin lakes and to the reputation which they have earned for escaping from nets. Other species were used for comparative purposes.

APPARATUS AND METHODS

A tank 157.8 cm long, 69.5 cm high, and 66.4 cm wide was used for these experiments (Fig. 1). Two opaque plastic partitions were placed near both ends of the tank. These partitions formed compartments which contained the drain pipe and water tap. The tank was uniformly illuminated by two fluorescent lights which were suspended from above.

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A frame on which various kinds of netting could be hung was constructed so that it tightly opposed the sides and bottom of the tank. Escape routes were provided in the netting either near the top or near the bottom of the frame. The net frame was immersed and withdrawn from the water by means of a cable, pulleys, and an electrically reversible motor. The net frame was attached to a carriage which moved along a track on the rim of the tank. The carriage was

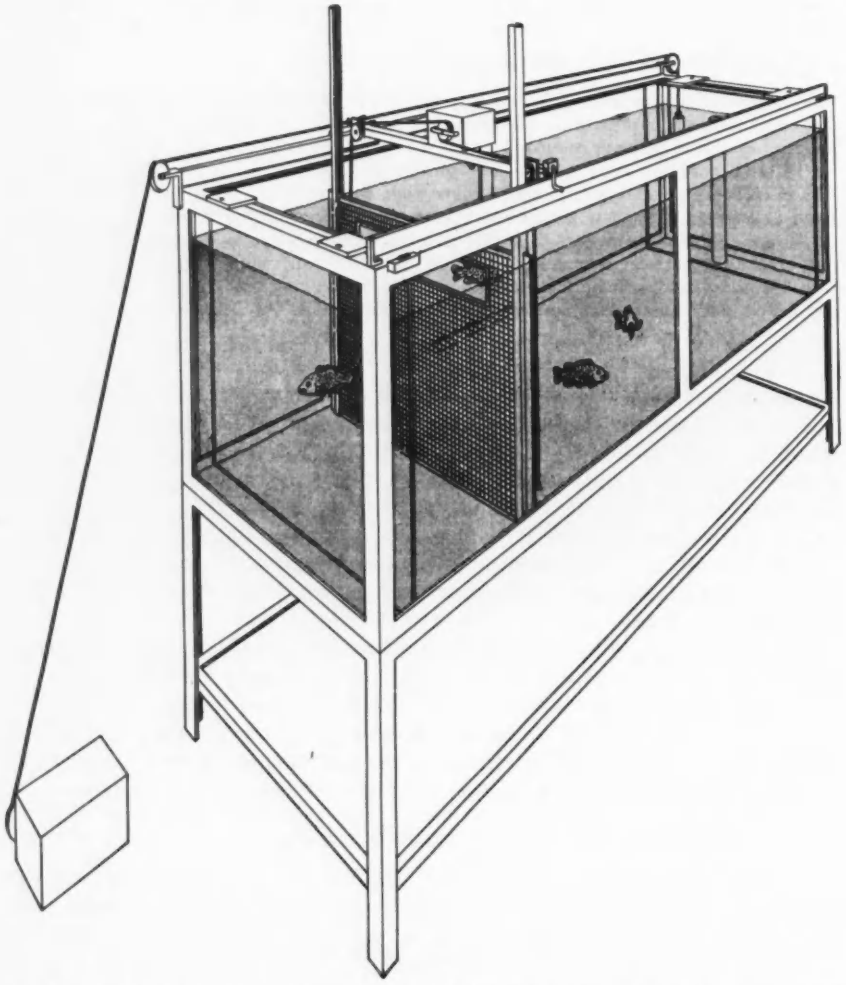

FIG. 1. Apparatus for studying the net-avoidance behavior of fishes. In the figure, net frame and carriage have traversed two-thirds of the distance to the punitive end of the tank. An escape route is located at the top of the net. Although plastic partitions at the two ends of the tank are shown as transparent in the apparatus, they were actually opaque.

moved to one end of the tank at a velocity of 2.1 cm/sec by means of a motor, cable, and pulleys. A microswitch stopped the forward progression of the carriage and an electric clutch, when disengaged, permitted the force of a weight to slide the carriage back to its position at the other end of the tank. All operations of net frame and carriage were synchronized by a cam timer which had a 4-min cycle. An operations recorder was synchronized with the apparatus such that the duration of each trial was marked on a chart and the observer could, by pressing a button, register the time at which each fish escaped.

Fish were placed in the tank and allowed to remain in the new environment until they behaved in a manner similar to that which was observed before they were transferred. As the net was pulled by the motor, fish were driven towards one end of the tank. The net progressed 120 cm until it stopped at a point 3 cm from the end of the tank; this end was designated as the punitive end. Fish that had not escaped by the time the net had stopped were exposed to the traumatic experience of being held for 60 sec in the 3-cm space between the plastic partition and the net. After the 60-sec period, the net was removed from the water and the carriage slid back to its original position against the plastic partition at the nonpunitive end of the tank. This constituted one trial. The interval between trials was 2 min.

The mean scores of the fish in seconds or the number of fish which escaped through an escape route while the net was moving was used for graphic presentation. These data were tested statistically by applying the chi-square test for two independent samples. The classes used for these calculations were: the number of fish which escaped the moving net; the number of fish which escaped while confined between the plastic partition and the net; and the number of fish which failed to escape during the entire trial. Separate calculations were made for each consecutive block of five trials.

Duplicate observations on the same fish inflated the number of observations, thus impairing the functioning of the chi-square test. For this reason, the statistical evidence was usually omitted from the presentation of our data. In all cases, however, the statistical evidence was in agreement with the observations made of the performance of the fish.

STIMULUS FOR ESCAPE

The aim of this study was to determine the features of the test environment which provided the stimulus that elicited escape behavior. Although at first carp did not attempt to escape the moving net, but swam in front of it, their behavior soon changed; they manoeuvered into a position in front of the escape route and darted through the hole.

The stimulus which evoked escape behavior could be one of the following: (a) the fish escaped the net when a certain distance was obtained between the moving net and the punitive end of the tank; (b) the fish escaped when the net had moved a certain proportion of the total length of the tank; (c) the fish escaped the net when a certain distance was obtained between the moving net and the

nonpunitive end; and (d) the fish learned certain landmarks on the side of the tank and swam through the escape route when the net reached this point.

The importance of these factors was evaluated by testing a group of carp in tanks of various lengths and comparing the regions in which they escaped. In three separate experiments the tank was shortened from the standard length of 120 cm to lengths of 95 cm, 105 cm, and 110 cm. This was accomplished by moving the plastic partition 25 cm and 15 cm away from the nonpunitive end of the tank and 10 cm away from the punitive end, respectively.

On each day of the experimental period the fish were subjected to 20 trials, 10 of which were conducted in the tank of standard length (120 cm), and 10 of which were conducted in a tank which was shorter than standard length. These two blocks of trials were alternated each day. The experiment was conducted for four days in the case of the 95-cm tank and for 14 days in the case of the other two experiments.

All experiments were performed with a single group of five carp which had been previously trained to escape the moving net through an escape route located at the top of the net. Experiments were conducted in cold water (11–14°C) with a net which had a hole at the top.

As a precaution against side effects caused by moving the plastic partition and to avoid the lower levels of performance during the first part of each testing session, only the last five trials of each block of 10 trials were evaluated. Scores, the seconds elapsed from the start of a trial until the fish escaped, were analyzed by means of a chi-square median test. Subsequently, for graphic presentation, the scores were converted to centimeters, that is, the distance the net had travelled when the fish escaped. To convert the data to centimeters, the time at which a fish escaped was multiplied by 2.1, the speed of the net in centimeters per second.

There was no significant difference among the medians in the three controls (tank length — 120 cm). Two of the medians were located in the same interval,

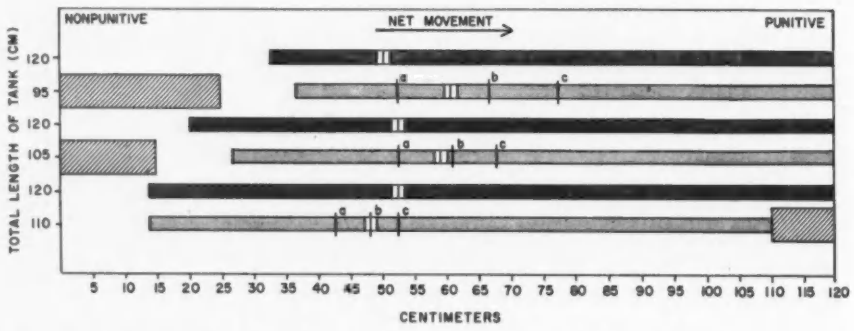

FIG. 2. The range and median of scores of a group of five carp tested in tanks of four different lengths. Diagonal blocks show lengths of tank excluded in each experiment; black bars represent range of scores in the standard length tank (control) and stippled bars range of scores in shortened tank; white band indicates the median class, and line in band the midpoint of class. Points a, b, and c are locations of hypothetical medians.

25 sec (52.5 cm), and the other median was located at 24 sec (51.4 cm). In each experiment, however, a highly significant shift in the distribution of scores resulted when the tank was shortened. Shortening the tank at the nonpunitive end caused the median to shift towards the punitive end, and shortening the tank at the punitive end caused the median to shift towards the nonpunitive end of the tank (Fig. 2). Since the median score changed significantly when the tank was shortened, it is doubtful that landmarks on the wall of the tank, hypothesis (d), played a role in determining the location in the tank at which the carp escaped.

In Fig. 2, marks are shown which correspond to the place the median would be expected to fall if the fish tended to: (a) escape at a constant distance from the punitive end of the tank; (b) escape in a position relative to the total tank length; (c) escape at a constant distance from the nonpunitive end of the tank. The scores of the controls from the three experiments were pooled and these data were used to determine the position of the three marks.

Of the three hypotheses, the second seems to be the most tenable since in all three experiments with a shortened tank, the median fell closest to that mark (b) which was located in the same relative position as the median in the control experiments. In order to provide additional evidence for this conclusion, the probability levels for each hypothetical median were determined. The data from each experiment were divided into two parts at the hypothetical median. The number of observations in each of these classes and the number of observations which fell above and below the actual median were entered in a contingency table. These values were then compared statistically using a chi-square test. The results show that the preferable hypothesis is that the fish do not maintain a specific distance from any one end of the tank but tend to escape in the same position relative to the dimensions of the tank (Table I). The fish may be inhibited by the lack of space between the net and the nonpunitive end of the tank and motivated to escape by the lack of space between the advancing net and the punitive end of the tank. If the fish are consistent in their adjustment to these two factors, it would be expected the fish would tend to escape at the same relative position in tanks of all sizes.

TABLE I. Probability levels for three alternate hypotheses for factors influencing position in tank at which a group of carp escaped a moving net.

	Probability levels for hypothesis		
Tank size	Proportional	Constant distance to nonpunitive end	Constant distance to punitive end
cm			
95	$.05 > P > .02$	$P < .001$	$.01 > P > .001$
105	$P \simeq .50$	$P < .001$	$.01 > P > .001$
110	Median falls in same interval	$.01 > P > .001$	$P < .001$

ROLE OF TEMPERATURE IN NET-AVOIDANCE BEHAVIOR

Studies were undertaken to determine if there were a differential choice of escape route between carp tested in cold and in warm water. Five groups of five carp each, which had been held at 11°C, were trained at this temperature during 25 trials to escape a net with holes across the entire top and bottom of the net. Five groups of five fish each, which had been held at 24°C for over two weeks, were trained in the same manner at 24°C. The choice of escape route and the time at which each carp escaped was recorded during each trial.

Upon introduction to the tank, the groups of carp usually formed a loose school located 16–32 cm from the bottom of the tank. Occasionally, the fish did not behave in this manner but aggregated in a dense mass on the bottom. In these experiments this was observed only in the fish held in warm water, but we have observed the same behavior at other times in cold water. Groups which behaved in this fashion nearly always chose the bottom escape route regardless of the water temperature at which they were tested. These fish were considered to be extremely frightened and their scores were separated from the scores of other groups.

In unfrightened carp, there was a distinct difference in the choice of escape routes between fish tested in warm and in cold water. The five groups of carp tested at 24°C most often used the top escape route when escaping the moving net while the five groups of carp tested at 11°C showed a marked preference for the bottom escape route (Table II). This difference was evident during the first trial. Of the 25 fish trained in warm water, 15 escaped the moving net through the top escape route and only four escaped the moving net by means of the bottom escape route. On the other hand, none of the 25 carp trained in cold water escaped through the top of the moving net on the first trial while 18 escaped through the bottom route.

TABLE II. The effect of temperature on the choice of escape route of groups of five carp tested for 25 trials.

Temperature:		11°C	24°C	24°C
Type of aggregation:		loose school	loose school	clumped
Number of groups of five carp tested:		5	5	3
Number of times fish escaped moving net	Top:	32	534	46
	Bottom:	474	39	315
Number of times fish failed to escape moving net		119	51	14
Number of observations		625	624	375

During the summer, carp can often be seen swimming near the surface of lakes in southern Wisconsin, often breaking the surface, and sometimes leaping completely out of the water. We have never observed carp behaving in this manner during the fall and winter when the water temperatures are considerably

lower. Selection of a bottom escape route in cold water and a top escape route in warm water may be a reflection of the general behavior pattern observed in the field during the winter and summer months.

Species of fish other than carp also tend to remain closer to the bottom at cold water temperatures than at warm water temperatures. Juvenile brown trout, *Salmo trutta* L., remain closer to the bottom during winter months than during the summer (Hartman, 1962); and captive schools of anchovies swim closer to the bottom when the temperature of the tank is decreased (C. P. O'Connell, personal communication).

EXPERIMENTS ON SOCIAL BEHAVIOR OF CARP

The objective of the studies presented in the next four sections was to evaluate the social behavior of carp in terms of their responses to netting gear.

Behavior of Carp Trained Individually and Trained in Groups

The experiments reported in this section were designed to determine whether social behavior plays a role in the responses of carp to a moving net.

Fish were trained to escape a net with a hole located across the top of the net. Five groups of five carp each and nine individuals were trained at a water temperature of 22°C. At a water temperature of 10°C, nine carp were trained individually and 45 carp were trained in nine groups of five each. Each group and each individual was trained separately for 25 consecutive trials. Two weeks prior to training, fish which were to be trained at 22°C were removed from holding tanks at 10°C and placed in tanks at 22°C.

Groups were more successful in avoiding the moving net than were isolated carp trained at the same water temperature. Fish trained in groups more often escaped the net while it was moving, whereas carp trained individually more frequently escaped the stationary net or were captured. At 22°C, the difference between the scores of groups and individuals was fairly constant during the entire 25 trials (Fig. 3). On the other hand, the scores of groups and individuals

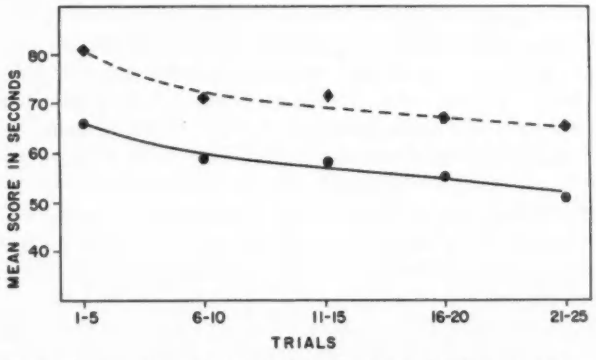

Fig. 3. Mean scores of five trial intervals for 25 carp trained in groups of five each (solid line) and nine carp trained individually (broken line) at a water temperature of 22°C.

trained at 10°C showed only slight differences during the early trials, but as trials progressed the fish trained in groups showed a distinct tendency to escape the net sooner than the carp trained individually (Fig. 4).

That there is a distinct difference in the choice of escape route between fish tested in warm and in cold water is further supported by the results of these experiments. Initially, carp trained in warm water escaped the moving net more frequently than did carp trained in cold water. In fact, not until trials 11–15 did the cold-water groups achieve the same level of proficiency that the warm-water groups had attained during the first five trials.

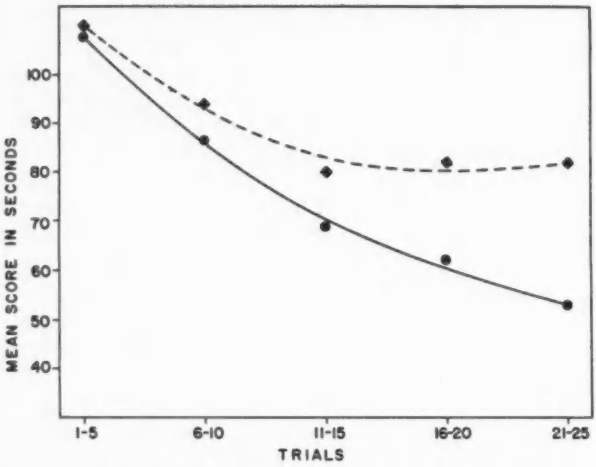

FIG. 4. Mean scores of five trial intervals for 45 carp trained in groups of five each (solid line) and nine carp trained individually (broken line) at a water temperature of 10°C.

EFFECT OF A TRAINED GROUP ON AN UNTRAINED INDIVIDUAL

The previous studies indicated that groups escape the net sooner than do isolated fish. The objective of this experiment was to determine if an untrained carp would follow a group of trained carp through a hole in a position which did not coincide with the fish's natural choice of an escape route.

A group of five carp was trained to utilize only the top hole of a net provided with escape routes at both the bottom and the top. Only rarely did one of the five trained fish fail to use the top escape route or fail to escape the moving net. During the course of the experiment, on only 27 out of the total 1875 trials did a trained carp escape through the bottom or become captured.

An untrained carp was added to the tank and tested with this group of five trained fish for 25 trials. This experiment was repeated 15 times with 15 different untrained carp. An additional 15 naive carp were trained separately without the group for 25 consecutive trials. These experiments were conducted at 13–15°C, and the net had escape routes located at both the top and the bottom.

Only rarely did an isolated carp escape through the top of the moving net. On the other hand, during each of the first five trials, two to four of the fish trained with the group escaped through the top opening while the net was in motion, and a maximum of eight did so during each of the last five trials (Fig. 5).

Each individual tested with the trained group immediately schooled with the group when placed in the test tank. The untrained carp swam with the group to a position a few centimeters from the net and directly in front of the top escape route at which time the trained group swam through the hole and the untrained fish either followed the group, turned away and escaped through the bottom route, or was captured.

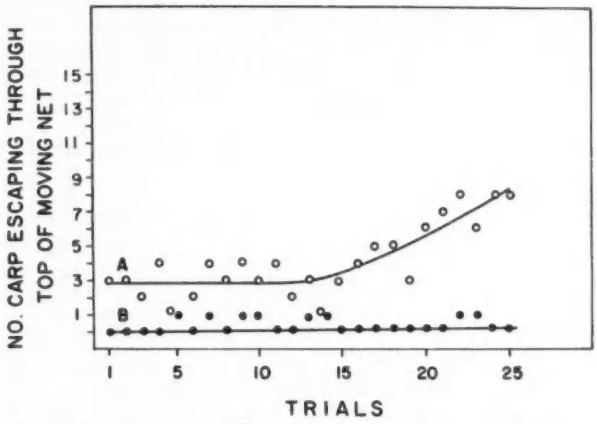

FIG. 5. Number of carp that used the top escape route when tested with a group which used the top route (A), and number of carp that used top escape route when tested alone (B).

It appears that the presence of a trained group was usually not a sufficient stimulus to induce an untrained carp to escape with the group through the top of the net but, rather, the natural tendency to escape near the bottom was followed. However, with repeated experience, fish more frequently escaped with the group.

During the last five trials of the experiment, there was a tendency for fish trained with the group to escape the net sooner than fish tested individually. This tendency was observed, however, only in the eight fish which escaped through the top escape route with the group and not in those fish which utilized the bottom route. Thus the mere presence of a group of carp did not appear to increase an individual's success in avoiding the net.

PERFORMANCE OF CARP TRAINED IN GROUPS BUT TESTED INDIVIDUALLY

The aim of this study was to determine if the members of a trained group of carp, when isolated, have the same success in escaping a net as when they are members of a group. This approach differs from the previous experiments in two

ways: first, in this study, fish were used which had been previously trained to escape the net, and secondly, each carp was tested under isolated and grouped conditions.

Tests were made on four groups of five fish each which had been previously trained to escape the net through the top escape route. On the day following the training period, each group was tested for five trials, then each member of the group was tested individually during five trials, and finally, the carp were again tested as a group. In this experiment, the identities of the fish were unknown. Another experiment was performed in which each fish could be recognized on the basis of natural markings or size and, consequently, we were able to tabulate the scores of each fish separately. Five carp which had been trained previously in a group to escape a net with a hole at the top were tested three times a week for 10 trials. A total of 17 tests was made. In 14 of these the fish were tested as a group; in three, each fish was tested separately. All experiments were conducted in cold water.

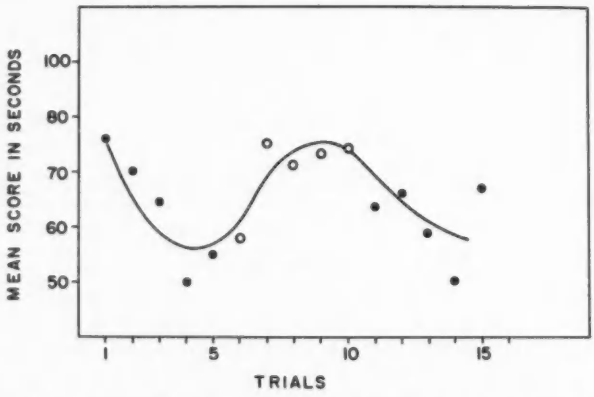

FIG. 6. Mean scores of 20 carp tested in groups of five each and tested individually. First five trials, fish tested in groups of five (closed circles); second five trials, fish tested individually (open circles); and last five trials, fish again tested in groups of five (closed circles).

In both experiments, the carp tested in a group were more successful in escaping the net than those tested individually (Fig. 6 and 7). There was no exact correspondence between those fish which escaped earliest when tested as a member of a group and those fish which escaped earliest when tested independently (Table III). In addition, when tested as a group, there was no one fish which consistently led the rest through the escape route. Even the fish that failed, when isolated, to escape the moving net on nearly every trial (No. V, Table III) was the first fish in the group to escape the moving net on six occasions.

The above results suggest that "following" may not be the only factor responsible for the greater success of groups in avoiding a moving net.

TABLE III. Mean scores of five carp when tested individually and when tested as a group and the order at which they escaped when tested as a group.

Fish	Mean score		Number of times each fish escaped in the given order					
	Group	Individual	1st	2nd	3rd	4th	5th	Captured
	sec	*sec*						
I	25.8	33.6	17	27	28	44	33	1
II	23.8	40.6	19	37	34	28	32	0
III	22.9	46.4	38	31	25	23	23	7
IV	24.7	88.9	66	28	18	14	17	6
V	30.6	117.2	6	26	45	32	15	25

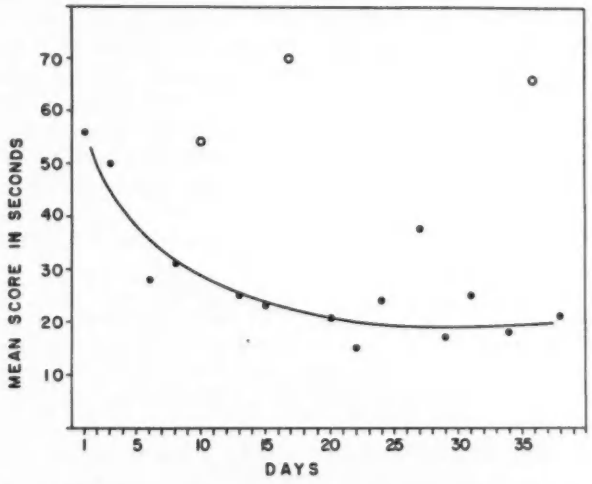

FIG. 7. Mean scores of a group of five carp tested as a group for ten trials on 17 different days (dots), and tested individually for ten trials on three different days (circles).

DISCUSSION

Groups of carp were shown to be more successful in avoiding a moving net than were isolated carp. This was demonstrated in both trained and untrained fish. The results of experiments conducted by Welty (1934) and by Hale (1956) are in agreement with our findings. Welty showed that goldfish traversed a maze more quickly when they were in groups than when they were isolated. Hale found that, in a maze, the performance of groups of green sunfish, *Lepomis cyanellus*, was faster and more uniform than the performance of isolated fish.

The factors responsible for the shorter reaction times of fish tested in groups have not been systematically investigated. However, Welty asserts that three factors are involved: (1) group cohesion, (2) reduced disturbance from outside

stimuli, and (3) increased exploratory activity. Hale, on the other hand, attributes the rapid performance of *Lepomis* tested in a group primarily to a type of "mutual stimulation". He found when "leadership" was experimentally reduced or eliminated, all of the fish still reacted much faster tested in a group than did any single fish tested alone. He also noted that the scores made by fish in isolation bore little or no relationship to the scores of the same fish when tested in a group. The same conclusions may be drawn from the study on individually marked carp presented in this report.

Groups of carp trained in warm water immediately showed faster reaction times than did individual carp trained at the same water temperature. On the other hand, with groups of carp trained in cold water, social factors did not appear to influence the performance of the fish until the last half of the training session. Similarly, not until the last segment of the experiment did carp tested in cold water with a trained group begin to escape with the group. One explanation for the delay in the appearance of social behavior at cold-water temperatures is that some element of the social behavior of carp is temperature dependent. Hale (1956) mentions that the stimulus value of fish appears to be a function of its level of activity. Since, in general, carp are less active in cold water than they are in warm water, it seems possible that the reduced activity of the fish is responsible for the delayed appearance of social behavior in the experiments conducted at cold-water temperatures.

OBSERVATIONS ON THE MASSING RESPONSE OF CARP

Groups of carp, when intensely frightened, collect in a dense mass on the bottom of the tank. The fish rest with their bellies and their pelvic and caudal fins touching the bottom and are so densely aggregated that the bodies of adjacent fish are in contact. A slight disturbance will change such an aggregation from an immobile mass to one of great activity. Those fish on the periphery of the aggregation swim over the mass and push their way in between the more centrally located fish. This movement may continue for a considerable time. The carp appear to seek contact with both the bottom and with other fish.

Carp which behave in this manner used a bottom escape route exclusively regardless of water temperature. In addition, if a bottom escape route was available, the frightened fish escaped the net more rapidly than did unfrightened fish. However, the performance of such fish did not change during a training session. The fish did not swim in front of the net but, rather, as the net approached, the group suddenly burst into activity and, without hesitation, the fish darted through the escape route. Carp newly procured fron the field often behaved in this manner as did fish which had been handled roughly.

We attempted to curtail this response by placing obstacles in the tank such that no more than two or three fish could line up side by side. The fish then aggregated above one another. The obstacles were removed after one week, at which time the fish resumed their former behavior. Adding a few unfrightened carp to the group did not change the response of the group but, instead, after a few days, the originally unfrightened fish behaved in the same manner as did

the group. Our only success in eliminating this response was to isolate the fish in separate tanks in pairs or groups of 2–3 fish; after a week the carp no longer showed the massing response.

If another carp was not present, a frightened carp remained as close as possible to a fish of another species. We introduced goldfish, *Carassius auratus*, white bass, *Roccus chrysops*, and large bluegill, *Lepomis macrochirus macrochirus*, into a tank containing a frightened carp. In these cases, the carp remained as near as possible to the strange fish and followed it throughout the tank. The white bass and goldfish did not appear to react to the presence of the carp. On the other hand, the bluegill responded to the carp by swimming away; nevertheless, the carp still remained very close to the bluegill.

The aggregation of carp into a dense mass in holding ponds has been described by carp seiners. These fishermen stated that the net tends to slide over their backs in the same manner that it would over a large stone.

ROLE OF VISION IN NET AVOIDANCE

These experiments were designed to evaluate the role of visual stimuli in the avoidance of nets. By the addition of India ink to the water or by the blinding of the carp, visual stimuli were reduced or eliminated.

Two groups of 20 fish each were trained to escape through a net with an 8-cm hole located across the top of the net. When nearly all of the fish escaped on each trial, an experiment was initiated to test their ability to avoid a net under turbid conditions. Five trials were conducted, at which time India ink was added to the water, thereby reducing the visibility in the tank to a few centimeters; ten trials were then conducted under these conditions. The two groups of carp were tested three times each using this procedure.

Three groups of 20 fish each were trained to escape through a hole which was located at the top of the net. After training had been completed, half of the carp from each group were blinded. In each group, the blind fish and the fish with unimpaired vision were tested simultaneously for 25 trials. A different method of blinding was employed for each of the three groups. They were as follows: (1) removal of the eye capsule; (2) cautery of the eye; and (3) placement of an opaque plastic cup over the eye.

In addition, a group of 10 carp which had no previous experience was blinded by removal of the eye capsule and afterwards trained to escape a moving net with a hole located at the top. As a control, another group of 10 inexperienced fish from the same holding tank was tested on the same day. At trial 18 the blind fish were given a mild electric shock for a short period after being caught; this was continued throughout the remainder of the experiment.

Groups tested under turbid conditions were less successful in avoiding a moving net when their vision was impaired by the presence of ink than when the water was clear (Fig. 8). As trials were continued under turbid conditions, the number of fish which escaped the net increased; however, the groups did not attain the same level of performance as was observed when the water was clear.

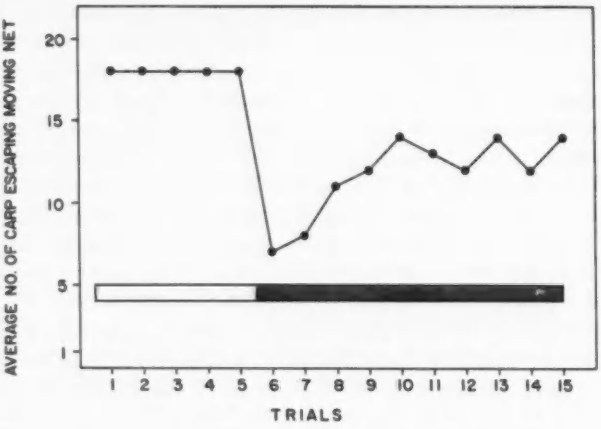

FIG. 8. The average number of carp (in two groups of 20 each, tested three times) escaping a moving net in turbid water. Black portion of bar indicates period fish were tested in turbid water.

Of the blinded fish which had previous training, more than half failed to escape the moving net on the majority of trials, whereas the fish with unimpaired vision tested with these fish nearly always escaped through the net (Fig. 9). In groups blinded by eye cautery and by eyecups, proficiency tended to increase during the training session. The scores of the carp blinded by eye capsule removal did not show this change.

Carp blinded prior to training were captured on each of the first 20 trials. On the other hand, all but one of the inexperienced fish with unimpaired vision avoided the moving net by the end of the experiment. The inexperienced blind fish, in contrast to all other blind fish, did not exhibit any searching behavior while confined. They did commence to search, however, when given an electric shock.

Some blind carp with previous experience escaped the moving net on the first trial while none of the inexperienced fish with normal vision escaped during the first trial. This suggests that some of the information gained while vision was intact was utilized after the fish were blinded.

The increase in the number of blind fish escaping through the net during a training period suggests that a new pattern of behavior may be developed under conditions where visual stimuli are not used. Observations of the blind carp provide some evidence which supports this view.

Carp with unimpaired vision usually swam toward the moving net, swam back and forth in front of the net, slowly approached the escape route and darted through. Blind fish were never observed to swim back and forth in front of the net. Indeed, they would often permit the net to push them toward the end of the tank; this never occurred in carp with normal vision. On the

other hand, when the net touched a blind carp the fish often moved rapidly up the surface of the net and sometimes escaped before the net stopped. During this movement, the fish never lost contact with the net; the fish touched its snout to the net and then its tail, and in this fashion moved up the net. Carp with unimpaired vision were never observed to behave in this manner.

Another difference between the behavior of blind carp and those with unimpaired vision was in their response to the net when they were fortuitously located in front of the escape route. Under these conditions, those with normal vision usually swam ahead of the advancing net and sometime later darted through the

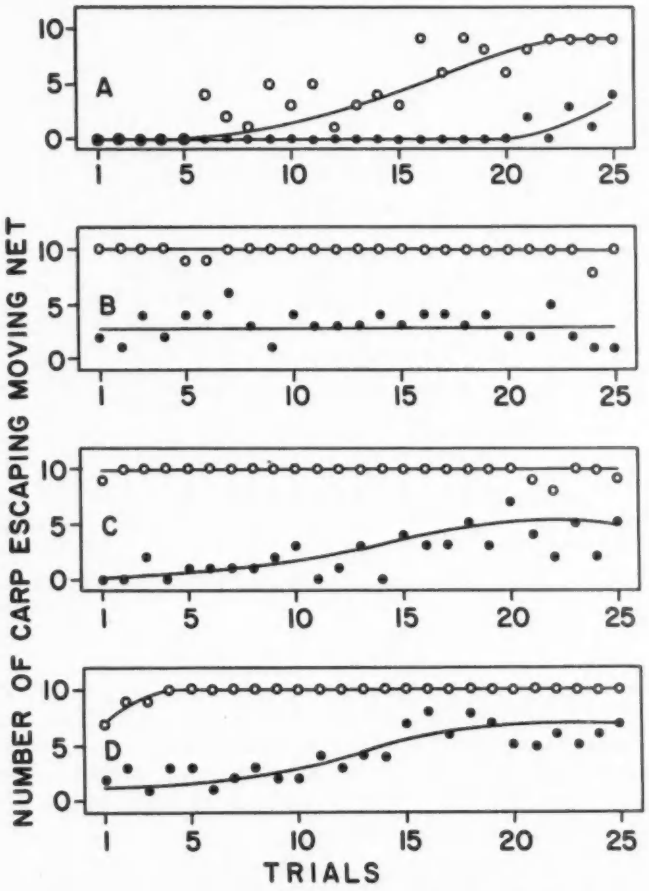

FIG. 9. Performance of four groups of 10 carp each with unimpaired vision (circles) and four groups of blind carp (dots): A, untrained carp blinded by removal of the eye capsule; B, trained carp blinded by removal of eye capsule; C, trained carp blinded by eye cautery; and D, trained carp blinded by placing opaque cups over the eye.

hole. Blind carp, on the other hand, did not show any observable change in behavior, the net passed, and the fish, without overt action, avoided confinement.

Some of the carp which had received intensive training responded to any disturbance, including the initial movement of the net, by swimming directly to the surface of the water. A few of the trained blind carp were also observed to behave in this manner and in some cases this facilitated their escape.

EFFECT OF PARTIAL OCCLUSION OF ESCAPE ROUTE BY AIR BUBBLES

A net with an escape route across the entire bottom of the net was constructed such that a row of air bubbles could be produced across either half of the escape route. Six groups of five carp each were used for this study; the testing and holding temperature was 15°C. During the first five trials of each experiment, the air bubbles were alternated from one side of the escape route to the other. Then, during the following 35 to 85 trials, the air-bubble obstruction was shifted from one side of the escape route to the other at five trial intervals. After this long training period, each group was tested again for five trials during which the air-bubble obstruction was again shifted on each trial. The portion of the escape route used by each fish and the time at which each fish escaped was recorded for the first and last five trials of each experiment.

These experiments indicated that carp avoided the band of air bubbles (Table IV). Only once did a fish escape through the band of air bubbles while the net was moving and this occurred after a long training period (30 trials) during which time the fish could have become familiar with the new stimulus.

TABLE IV. The use by carp of an escape route occluded with bubbles and one not occluded.

Period of observation	Number of times carp escaped				Number of times carp failed to escape
	Moving net		Stationary net		
	Occluded	Not occluded	Occluded	Not occluded	
First trial	0	19	2	7	2
First 5 trials	0	77	6	64	3
5 trials after a long training period	1	120	3	21	5

Use of the portion of the net which was obstructed by air bubbles was more frequent when fish were confined at the end of the tank. This is not surprising as at this time the carp were restricted to a small area and were in closer proximity to the bubbles.

NET-AVOIDANCE BEHAVIOR OF TEN SPECIES OF FISH

The objective of this study was to compare the responses of various species of fishes to a net in the experimental apparatus. At a water temperature of 13–16°C, 10 species were tested in groups which varied in size from 5 to 20 individuals. The lengths of these fishes were comparable to the lengths of carp

used in the previous experiments, i.e. approximately 80–200 mm. Only a net with a hole at the top was utilized in the studies of brown trout, rainbow trout and golden shiners. In the balance of the studies the fishes were also tested with a net which had an escape route located at the bottom. As a result of the study, the performance of each species in the test tank was rated using an arbitrary scale. Carp were given the value of one and northern pike the value of five. These fishes were chosen to set the limits of the scale because of all the fishes studied carp showed the greatest ability to avoid a net while northern pike the least. The rest of the species was assigned a position on the scale between one and five on the basis of their relative ability to escape a net. The values assigned to each species are shown in Table V; a summary of the information on which the ratings were based is also presented in Table V.

Of all fish studied, rainbow trout were initially the most successful in avoiding a net with an escape route at the top; over half of these fish escaped the net on the first trial. Carp, golden shiners, and brown trout were able to escape the moving net when an escape route was provided at the top but their initial success was not as great as the rainbow trout. With an escape route provided at the top of the net, pumpkinseed sunfish, northern bluegill sunfish, white bass, and northern largemouth bass only rarely escaped but, on the other hand when a hole was located at the bottom of the net these fish usually did escape.

In response to a disturbance near the tank there was a general tendency for all fish to swim towards the bottom. This reaction may be partially responsible for the greater use of a bottom escape route.

The manner in which each of the 10 species of fish avoided the net varied considerably. Carp, golden shiners, and largemouth bass swam towards the escape route, hesitated, and then, with a sudden burst of speed, darted through the hole. Rainbow trout, on the other hand, appeared not to respond to the moving net until they had been driven by the net to a position near the end of the tank. At this point these fish, in a frenzy of activity, darted wildly in all directions and in this manner escaped the net. Although the rainbow trout were tested only with a net with an escape route at the top, judging from the behavior of the fish it seems likely that they would have been equally successful in avoiding the net if an escape route had been provided at the bottom only. Common white suckers, when first touched by the net, occasionally showed a response similar to that of the rainbow trout, however, they were rarely successful in escaping the net. Brown trout appeared to respond to the net only when they were confined near the end of the tank. Their movements were not as frenzied as were those of the rainbow trout.

The responses of bluegill, pumpkinseed sunfish, and white bass to a net appeared to be more passive than the fish described above. No change in their behavior was observed either before, during, or after escape. Apparently confinement was not as strong a negative stimulus for these species as it was for the fish described in the preceding paragraph. When the escape route was at the bottom, white bass, bluegill, and pumpkinseeds that had escaped the net often swam back into the confinement area and joined the fish which were still trapped

TABLE V. Characteristics of the net-avoidance behavior of ten species of fish.

Species	Locomotor activity in tank	Escape routes used	Change in scores detected during training	Regions explored during confinement	Contact with moving net	Description of act of escape	Performance scale
Cyprinus carpio (carp)	very active	bottom and top[a]	present	all	rarely	active	1
Notemigonus crysoleucas (golden shiner)	very active	top[b]	present	all	rarely	active	1
Salmo gairdneri (rainbow trout)	very active	top[b]	no change	all	rarely	frenzied	2
Salmo trutta (brown trout)	moderately active	top[b]	present	mostly bottom and sides	tail only	active or frenzied	3
Micropterus salmoides (northern largemouth bass)	inactive	rarely top and bottom	present	mostly bottom and sides	rarely	mostly passive	3
Lepomis gibbosus (pumpkinseed sunfish)	inactive	bottom	present	bottom and sides	occasionally complete contact	mostly passive	4
Lepomis macrochirus (northern bluegill sunfish)	moderately active	bottom	present	bottom and sides	occasionally complete contact	mostly passive	4
Roccus chrysops (white bass)	moderately active	bottom	present	bottom and sides	rarely	frenzied or none	4
Catostomus commersonii (common white sucker)	inactive	rarely bottom	no change	mostly bottom	frequent complete contact	none	5
Esox lucius (northern pike)	very inactive	failed	no change	none	frequent complete contact	—	5

[a]See "Role of temperature in net-avoidance behavior" section.
[b]Ability to use bottom escape route not determined.

behind the net. During a study of bluegill the negative stimulus of confinement was strengthened by giving the fish an electric shock while they were restricted to the area between the net and the end of the tank. After shocking was commenced, the response of these bluegill to the net changed; their reaction appeared to be the same as or similar to the response of carp or largemouth bass.

A change in performance during a training session was most marked in groups of carp and golden shiners and, to a lesser degree, was present in largemouth bass, bluegill, pumpkinseeds, and brown trout. Although the rainbow trout were quite successful in evading the net, over half the fish escaped during the first trial, the proficiency of the group did not change over a period of 20 trials.

During the time the net was crossing the tank, many of the species avoided contact with the net. Carp, golden shiners, rainbow trout, and white bass always avoided contact with the moving net. On the other hand, bluegill, pumpkinseed sunfish, northern pike, and common white suckers were at times pushed along the bottom of the tank by the net.

Those carp, golden shiners, and rainbow trout which failed to escape a moving net, swam actively in all regions of the confinement area and struggled against the net and the sides of the tank. Only some of the members in groups of bluegill, pumpkinseed sunfish, white bass, and brown trout swam actively in the confinement area. The rest of the group remained relatively quiescent. Occasionally, just as the net stopped, largemouth bass and suckers swam rapidly to the surface. Thereafter the suckers remained on the bottom whereas the bass often continued to move about in the confinement area. When confined, northern pike neither struggled nor swam. These fish often did not change their position even after the net was withdrawn from the water.

These observations emphasize that in order for a netting technique to be effective it must be adapted to the behavior of the species of fish for which it is to be used. The behavior of carp and rainbow trout is a case in point. Both fish are highly successful in avoiding a net but do so in a different manner. A driving device such as a bubble net might be efficient in driving carp; on the other hand, it would probably be ineffective in directing the movements of rainbow trout. Once the trout commenced their frenzied avoidance behavior a band of air bubbles would probably not prevent their escape.

Both rainbow trout and carp were very active in the test tank. In general, it appeared that the more locomotor activity a species displayed the more successful the species was in avoiding a net.

INTERPRETATION

The application of these data to the carp fishery rests upon two assumptions: (1) the behavior of carp in the experimental apparatus is the same or similar to the behavior of carp under netting conditions in the field; and (2) the behavior of the juvenile carp which were studied in this investigation is similar to the behavior of adults.

There are indications that these assumptions may safely be made. Where it has been possible to make comparisons, observations in the field appear to agree with those made in the laboratory. These are as follows: (1) in southern Wisconsin waters carp are usually the most difficult fish to capture; (2) in holding ponds carp are reported to be able to avoid capture after one or two successive experiments with a seine, and consequently, the number of marked recaptures is very small; (3) in holding ponds carp have been observed to form dense aggregations of the kind described in this report; and (4) in turbid water carp do not swim ahead of the net; indeed, it is reported that their weight against the seine makes hauling of it difficult (C. Brant, personal communication).

The role of the sensory systems used by carp in the avoidance of nets was not fully explored. Evidence was presented which strongly indicated that when vision was possible, the fish relied upon visual stimuli. On the other hand, when vision was impaired by blinding or by turbid water some of the fish were still able to avoid the net. Observations on the behavior of fish under these conditions suggested that tactile stimuli play an important role when vision is impaired. The studies conducted by John (1957) indicate that blinded fish use stimuli other than tactile cues to avoid objects. Thus, water movement, sound, and low frequency vibrations may also play a role in the recognition of a net and in escapement. These factors, however, were not investigated.

The rigidity with which certain learned patterns of escape behavior were maintained by carp was remarkable. When an escape route had been provided in a net at the bottom, groups which had been trained to escape through the top of the net seldom used the bottom route. This was notable since, at the cold water temperatures at which these experiments were conducted, untrained fish nearly always chose a bottom escape route. When groups of carp were trained to escape through a small hole in the top corner of a net they continued to escape through this small space when the hole was expanded across the entire top of the net. On a few occasions a trained fish was placed behind the net at the beginning of a trial. When the net commenced moving away from the nonpunitive end of the tank these fish swam rapidly after the net and through the escape route. In a few cases, isolated carp did not learn to escape through a hole in the net but learned another behavior pattern. When the net approached, they swam rapidly to a corner of the confinement area near the surface of the water, and remained in this position until the net returned to its former location at the nonpunitive end of the tank. The pattern, once learned, was repeated even when other trained fish were added to the tank.

The rigidity with which these behavior patterns were maintained suggests that, in contrast to many of the species tested, confinement is for carp a very strong negative stimulus. We believe this, in part, explains the relatively greater success of carp in escaping a net.

An interesting aspect of the studies was the correlation between water temperature and the behavior of the carp. Water temperature appeared to influence the escape route utilized by carp, their locomotor activity, and perhaps, their social behavior. According to our observations, at cold-water temperatures

the fish tend to be less active, escape only through the bottom escape route, and perhaps are not as strongly influenced by the behavior of other carp in the school.

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NOTES

A Convenient Technique for Obtaining Pituitary Glands from Fish

During a general study of the hormones of salmon pituitary glands (Schmidt *et al.*, MS, 1963), it became apparent that a convenient and rapid technique for obtaining large numbers of pituitary glands was necessary. The methods in use have been laborious and generally involved a dissection and exposure of the brain followed by removal of the gland lying beneath it (Atz and Pickford, 1959). Others have used with success a meat-cutter's band saw to make the initial cut through the head (Atz and Pickford, 1959). While the latter method insures success for operating on smaller species of fish at convenient locations, it is not readily adaptable for larger fish under field-work conditions. A large butcher knife hinged on the cutting tip and operated like a paper cutter has been used to advantage (Burrows, personal communication) to make the initial cross-sectional cut through the brain area of the head.

Since inherent disadvantages existed in all of these methods a different technique was developed utilizing an adaptation of a laboratory cork borer to remove a core, one inch in diameter, from the head in the region of the brain. Basically, the apparatus (Fig. 1A) is a power- or a hand-driven borer with a movable piston for ejecting the core which is then sliced cross-sectionally with a knife; the brain tissue removed, and the pituitary gland collected with a suitably shaped probe.

The design of the cutter is illustrated in Fig. 1B. The cylinder (f) is constructed from tubular stainless steel 1 inch in diameter. The core ejection shaft (d) is made of stainless steel rod, with one end machined to fit snugly inside the cylinder. In its boring position the shaft is drawn up inside the aluminum collar of the cylinder as illustrated in (c) and locked in position by a spring-loaded pin that fits into a slot (e) in the shaft. The entire assembly is attached to and powered by a heavy duty $\frac{3}{8}''$ electric drill (Fig. 1A). The core is ejected by depressing the lever (g), releasing the pin, and pushing the shaft through the cylinder.

When electric power is not available, either a battery-powered drill or a hand-operated ratchet screw driver (a) can be used. With the screw driver assembly, the core ejection shaft (d) is replaced by one with a shorter shaft (b). When pressure is applied to the screw driver in the clockwise turn position, a turning motion imparted to the borer facilitates cutting. To eject the core, the ratchet is locked and the core ejector shaft is pushed through as previously

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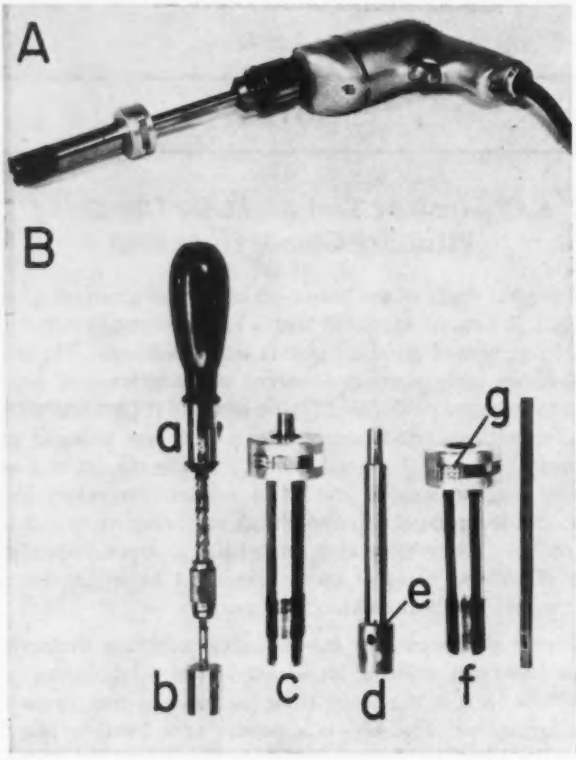

FIG. 1. A. View of cutter attached to power drill; B. an exploded view of the cutter constructed to specifications by Modern Engineering Co. Ltd., 1695 West 5th Ave., Vancouver 9, B.C.

described. For salmon up to 10 lb, the screw driver assembly was found to be the most convenient since one person can hold the fish as well as operate the borer under the most adverse field conditions. For larger fish considerable effort is required for cutting and the power-driven assembly is preferred. In this case another person is required to hold the fish in a special trough mounted on a saw-horse, as illustrated partially in Fig. 2A. Large-scale hatcheries conducting artificial spawning were selected to obtain the glands not more than 1 hour after death of the fish.

The angle at which the fish head is drilled is shown in Fig. 2A. The borer is held perpendicular to the top surface of the head at a position just behind the eyes and drilled through the bony gill arches located in the roof of the mouth. With little experience, well over 95% of the glands may be recovered with an average drilling time of 15 sec per fish.

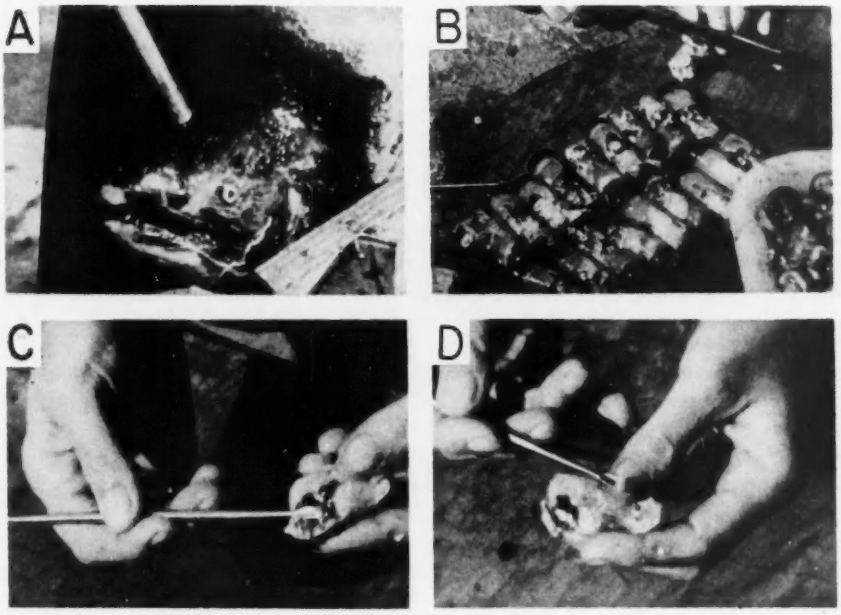

FIG. 2. A sequential illustration showing (A) the boring technique; (B) the knife-cut through the core; (C) the removal of the pituitary gland, and (D) the relative size of the gland from a chinook salmon.

Figure 2B, C and D illustrate the removal of brain and pituitary gland in a core obtained from the head of a chinook salmon (*Oncorhynchus tshawytscha*). The technique has also been successfully used for collection of fish brains. In a 4-week spawning season, using two of the drills described above, approximately 20,000 pituitaries and 10,000 brains have been collected and preserved by freezing in solid carbon dioxide.

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A Vacuum-Assisted Subsampler for Use with Small Planktonic Organisms

A vacuum-assisted subsampler (Fig. 1) was developed at the Institute of Oceanography, University of British Columbia, to obtain representative 10% portions from plankton samples of moderate volume, such as obtained by the Clarke-Bumpus sampler. The sample is kept mixed by stirring with the tube into which the subsample is drawn. The diameter of the opening of this tube restricts use of the subsampler to smaller organisms.

The subsampler consists of a glass tube connected to an aspirator by a length of flexible tubing fitted with a squeeze-bulb and a spring-loaded pinchcock. All connections are air-tight. The glass tube has an inside diameter of 14 mm which is constricted at its receiving end to 8 mm. It is calibrated to receive a volume of 10 ml. A sample is prepared for subsampling by removing the larger organisms and diluting the remainder with 10% formalin–seawater to 100 ml in a 150-ml beaker.

The subsampler is operated as follows. Flow through the aspirator is carefully adjusted until the required vacuum is obtained. The sample is thoroughly stirred to the bottom of the beaker by a figure-eight motion of the glass tube. While stirring continues, the receiving end of the tube is lifted to midway up the sample and the pinchcock is opened and closed quickly and precisely so that a 10% portion of the sample is trapped between the calibration mark and the receiving end of the tube. The subsample, held within the tube by surface tension and atmospheric pressure, is released over a sorting dish by compression of the squeeze-bulb.

The accuracy of estimation by this procedure is indicated by the statistics shown in Table I. A *t*-test of the difference between the mean obtained from seven subsamples and the number calculated as one-tenth of specimens counted in the whole sample was applied to three different samples containing only the planktonic ostracods *Conchoecia elegans* Sars and *C. alata major* Rudjakov (?) (since designated as *C. alata minor* McHardy (McHardy, 1964)) in their various

TABLE I. Significance of the difference between 10% of the specimens in a sample and the number of specimens in a 10% subsample of that sample — from seven subsamples of three samples containing only *Conchoecia elegans* Sars and *C. alata major* Rudjakov (?) in their various growth stages.

Sample		Subsample				
No.	Actual 10%	Mean	Standard deviation	Error of mean	Standard error of mean	*t*-value ($t_{.05} = 2.45$)
			Conchoecia elegans Sars			
1	5.3	7.0	1.76	+1.7	0.72	2.36
2	11.2	9.7	2.19	−1.5	0.89	1.69
3	20.3	22.1	3.55	+1.8	1.45	1.24
			Conchoecia alata major Rudjakov (?)			
1	10.7	9.7	2.70	−1.0	1.10	0.91
2	34.0	37.1	6.18	+3.1	2.52	1.23
3	36.4	39.0	6.97	+2.6	2.84	0.92

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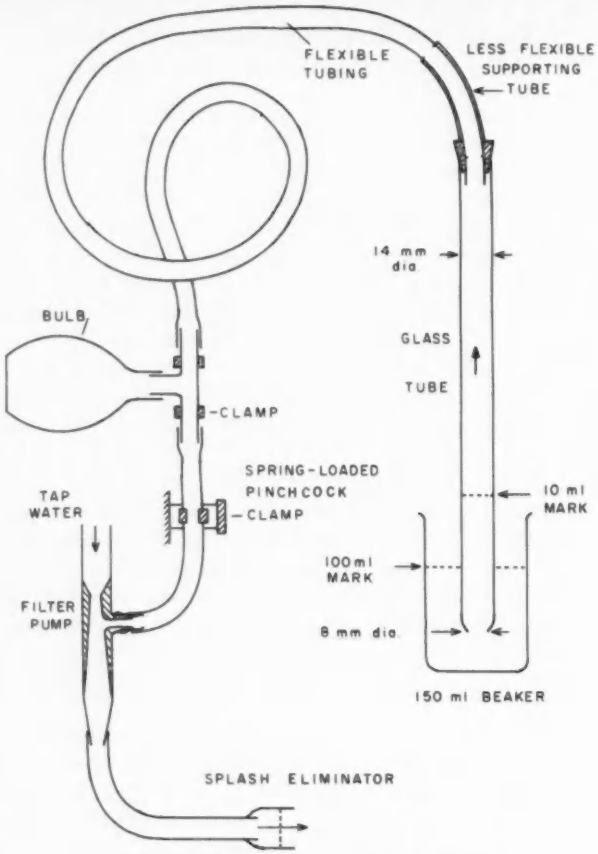

FIG. 1. The vacuum-assisted subsampler.

growth stages. The differences due to subsampling were not significant at the 0.05 level of confidence.

It is recommended that the subsampling differences be compared with variations due to sampling error and population difference, and that the subsampler be retested for use with organisms which are rather different from those tested here.

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Amino Acid Composition of Bacteria and Its Possible Relation to Taxonomy

Recent studies have demonstrated that the composition of a number of chemical components of bacteria can be usefully correlated with the criteria which are usually applied to bacterial taxonomy (Marmur *et al.*, 1963). The most extensively investigated bacterial components are the deoxyribonucleic acids where the base compositions (usually expressed as guanine-cytosine content) are known to be similar in taxonomically related bacteria (Belozersky and Spirin, 1960). Sueoka (1961) has analysed partially purified protein preparations from a number of species of bacteria and found that there is good correlation of the amounts of *some* of the amino acids present in the bacterial protein preparations with deoxyribonucleic acid base composition, the regression relationships being extremely significant for the correlation of the amount of guanine plus cytosine in deoxyribonucleic acid with the amounts of each of the amino acids arginine, alanine (positive regression coefficients), isoleucine, and phenylalanine (negative regression coefficients). Stewart *et al.* (1963) have recently reported the total amino acid compositions of a number of species of bacteria. It is consequently of interest to examine the relationship of the total amount of each of the amino acids, alanine, arginine, isoleucine, and phenylalanine, to the amount of the same amino acid in protein of each of the species of bacteria for which comparable analyses are available. The data for the six species for which this is possible are presented in Table I. The values for total amino acid content

TABLE I. Comparison of (A) total bacterial content of different amino acids with (B) content of same amino acids in partially purified protein. Quantities expressed as moles per cent of stable amino acids (Sueoka, 1961).

	Alanine		Arginine		Isoleucine		Phenylalanine	
Bacterium	A	B	A	B	A	B	A	B
Bacillus cereus	18.3	14.1	5.8	6.0	6.3	9.6	7.5	5.3
Escherichia coli	16.1	14.6	7.5	7.4	7.4	7.5	5.3	4.9
Aerobacter aerogenes	15.2	15.7	7.5	6.8	6.9	7.1	4.5	4.5
Serratia marcescens	15.5	15.5	7.0	6.7	6.7	6.3	5.3	5.4
Sarcina lutea	23.9	17.7	5.8	9.8	3.6	5.0	2.5	3.8
Pseudomonas aeruginosa	15.8	15.9	7.9	8.4	6.2	6.5	4.8	4.7

(Stewart *et al.*, 1961) have been converted to the same units (moles per cent stable amino acids) as are used in Sueoka's data. It can be seen that there is a correlation between the values of Stewart *et al.* (1963) and those of Sueoka (1961) for the three amino acids, alanine, isoleucine, and phenylalanine, with correlation

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coefficients of 0.81, 0.63 and 0.88, respectively. Since Sueoka (1961) has shown a significant relationship between the amounts of these amino acids in the protein of a bacterium and the base composition of the organism's deoxyribonucleic acid, which, in turn, has been correlated with other taxonomic criteria, the implications of the further correlation with total amount of certain amino acids are obvious. It would be of interest to further explore such a possible taxonomic relationship in other species of bacteria and in other organisms for which a considerable range of deoxyribonucleic acid base compositions has been demonstrated, e.g. protozoa.

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Angling License Sales from Northwest Territories, Canada, with Special Reference to Great Slave Lake

Increases in travel facilities and tourist publicity have stimulated angling in the Northwest Territories. The tourist, Sivertz (1961) predicted, will ultimately provide the second largest northern industry. Information secured from angling licenses, the only obtainable quantitative data, is therefore presented to document the sport fishery of an earlier period.

Northwest Territories resident and non-resident angling licenses are issued on an annual basis (April 1 to March 31) by the Department of Fisheries of Canada. They are obtained from fishery officers, Royal Canadian Mounted Police, selected merchants, and fishing lodge operators. Licenses were introduced in 1950; angling permits had been required previously, but were discontinued in 1946.

The sales records and all extant licenses for 1950–51 to 1961–62 were examined. The place of issue for all but 15 licenses was ascertained, but other details usually were available only for the Great Slave Lake licenses.

During the first 12 years, 7603 licenses were issued (Table I). Generally, sales have increased annually but at an uneven rate. Licenses were obtained at numerous locations. However, the greatest number (approximately 3300 or 43%) were secured at radar sites. The DEW Line, situated along Latitude 70°N, was started in December 1954 and became operational on July 31, 1957. The other concentration of licenses (3058 or 40%) came from the Great Slave Lake region. It therefore has received the greatest tourist angling pressure.

At Great Slave Lake licenses were issued at Hay River, Yellowknife, and at lodges at Taltheilei Narrows and Snowdrift. The yearly trends for the three groups of licensees were generally similar (Table II). Persons residing in Canada accounted for three-fifths of these licenses, two-fifths of which went to territorial residents only. Alberta residents purchased 75% of 650 licenses issued to Canadians living in the provinces. The two largest cities, Edmonton and Calgary, had a total of 240 licenses. Ontario was second with 57 licenses, followed by Saskatchewan (40), British Columbia (34), and Manitoba (31). There was a greater diversity of origin for 1144 licenses issued to Americans. Only 11 states, mostly from the southeastern seaboard, were not represented. Residents of 22 states received from 1 to 19 licenses; those from 17 states received 20 or more licenses. The greatest number (148 or 13%) was purchased by Illinois residents, followed by Minnesota with 129 licenses and Texas with 108. Large cities did not have dominant representation. The most for any city was 39 (Houston, Texas). The distribution of American licensees appears to have been related to the promotional activities of the fishing lodge operators.

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TABLE I. Northwest Territories angling licenses from 1950–51 to 1961–62 according to place of issue. The percentage of non-resident licenses is in parentheses.

Location	N Lat.	W Long.	Year											Total
			51–52	52–53	53–54	54–55	55–56	56–57	57–58	58–59	59–60	60–61	61–62	
Aklavik[a]	68°12′	135°00′	...	...	...	...	4	...	...	22	52	50	32	160 (53)
Baker Lake	64°18′	96°03′	...	...	...	...	...	4	15	15	24	29	41	128 (30)
Cambridge Bay	69°03′	105°05′	...	...	...	...	49	9	12	10	34	63	88	265 (58)
Cape Christian	70°27′	68°33′	...	...	...	...	3	9	...	4	7	5	20	48 (10)
Cape Parry	70°10′	124°41′	...	...	...	...	...	4	...	19	15	11	6	55 (22)
Chesterfield Inlet	63°25′	90°45′	...	...	...	2	...	10	12	3	12	11	11	61 (62)
Coppermine	67°50′	115°05′	...	...	...	...	...	13	11	5	14	10	9	62 (37)
Eskimo Point	61°07′	94°03′	...	...	...	...	8	...	11	7	1	3	2	32 (81)
Frobisher Bay[b]	63°44′	68°28′	...	...	...	...	...	489	626	735	572	427	451	3300 (80)
Rankin Inlet	62°45′	92°10′	...	...	...	...	...	...	...	...	15	32	40	87 (28)
Fort Smith	60°00′	111°53′	...	...	...	...	...	...	...	...	9	48	89	146 (37)
Subtotal[c]			...	3	...	2	64	538	687	820	762	726	928	4530 (71)
Great Slave Lake	61°23′	115°38′	112	77	103	128	206	205	152	279	441	677	678	3058 (64)
Total[d]			124	80	103	132	270	743	839	1099	1203	1403	1606	7603 (68)

[a]Includes Inuvik (68°21′N, 133°43′W).
[b]Includes Distant Early Warning Line sites.
[c]Includes 104 from 9 other locations and 82 from Great Bear Lake in 1961.
[d]Includes 15 from unknown locations, one being issued in 1950.

TABLE II. Northwest Territories angling licenses issued at Great Slave Lake according to residence of licensees. The number of states is in parentheses.

Year	Canada		U.S.A.	Total[a]
	N.W.T.	Provinces		
1951–52	46	30	11(4)	112
1952–53	31	26	20(8)	77
1953–54	25	28	50(11)	103
1954–55	25	21	82(17)	128
1955–56	99	26	81(15)	206
1956–57	88	24	9(5)	205
1957–58	84	29	39(12)	152
1958–59	162	75	42(14)	279
1959–60	153	120	168(27)	441
1960–61	199	119	359(33)	677
1961–62	243	152	283(32)	678
	1155	650	1144(40)	3058

[a]Includes 109 licenses of unknown residence.

It should be pointed out that the above figures do not include all people who fish in the Northwest Territories since persons who live and work in remote areas are allowed to take normal food supply without a license. The above analysis does however indicate the general distribution and angling in the Northwest Territories and the origin of the anglers.

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Bathythermograph Data on Aperture Cards: A New Approach to an Old Problem

In contrast to recent technological advances in the automation of oceanographic data processing, the methods of handling bathythermograph data have remained virtually unchanged during the past 25 years. The format of the bathythermograph record has restricted the ease of processing and reproduction of the slides, and prevented rapid data retrieval and fast sequential examination of the information.

LaFond's (1951) standardized method of processing bathythermograph data has been widely adopted by most laboratories throughout the world. In his concluding remarks, LaFond stated that the accumulation of large quantities of data would eventually require punched-card systems. Today, although large volumes of bathythermograph data exist, no punched-card system has been developed that preserves the temperature–depth relationship of the original trace. As a result, analytical work based on bathythermograph data in large-scale environmental investigations has reached the stage where most oceanographic laboratories consider such studies beyond the capabilities of their existing staff. The problem continues to grow with each new bathythermograph trace and yet, in many areas of the world oceans, the bathythermograph (Spilhaus, 1938) is providing the only means of collecting oceanographic information.

The urgency of the need for full exploitation of the existing bathy-files has necessitated a critical examination of the existing processing systems. In reviewing these methods, it became evident that the record format needs revision, and that the ultimate format to be selected largely depends on the requirements of the user. The bathythermogram in its present form constitutes a trace on a 1×1.75-inch smoked (or gold-plated) glass slide, and when superimposed on a corresponding transparent calibration grid and adjusted for instrumental errors, it provides a continuous graphical record of water temperature versus depth. These are generally stored as photographic records and constitute the existing bathy-files.

Present opinions are divided on this mode of storage, in that some favour filing a digitized trace, while others insist on the preservation of the original continuous record. The advantages of the former lie in the capability of high-speed magnetic-tape data handling, while the latter embodies the preservation of the complete original temperature trace.

The system being introduced into the Canadian oceanographic community lends itself to current high-speed data-processing techniques, while preserving the storage aspects of the original bathythermograph trace. It essentially duplicates LaFond's standardized method of processing bathythermograph data, except that complete automation of the photographic process is achieved by a

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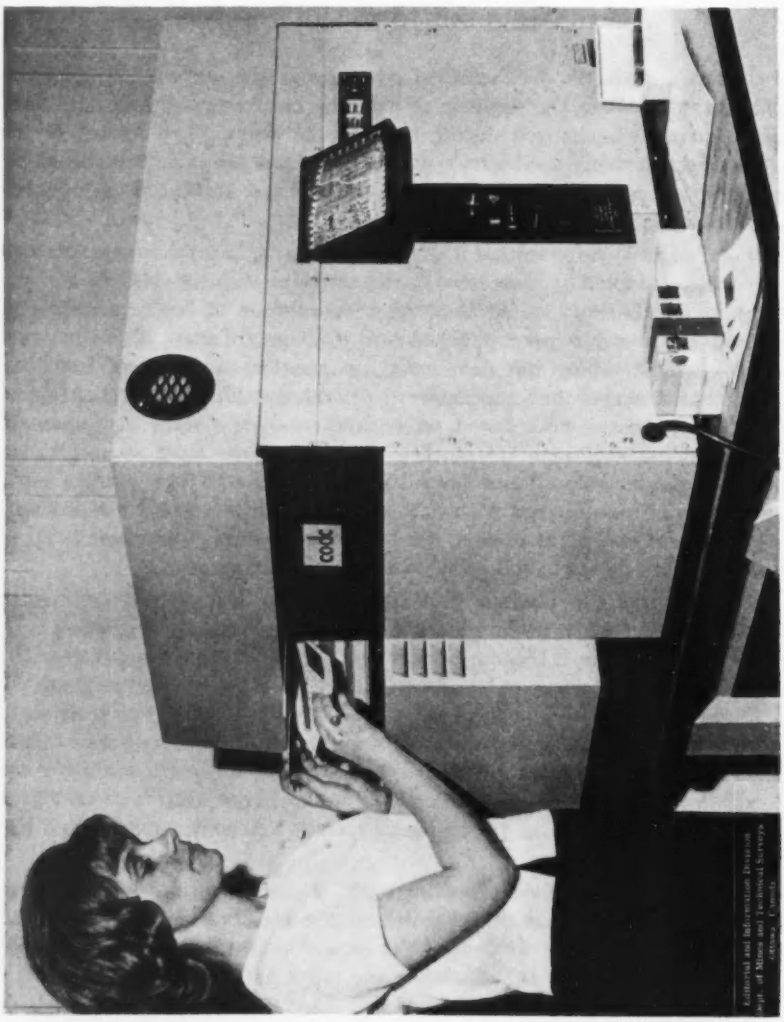

FIG. 1. The Bathythermograph Card Processor. The photograph shows the operator removing one of the aperture-cards which was produced in 50 seconds after feeding the grid/slide combination into the right-hand side of the Processor.

modified commercially available camera[1] which transposes the bathythermograph record directly to an aperture frame punch-card[2] (hereafter referred to as a "bathythermograph aperture card").

The modification, comprising a complex viewer assembly, was developed by the National Research Council of Canada. The complete unit is referred to as a Bathythermograph Card Processor (Fig. 1). Two controls and a viewing unit enable the operator to make all the required adjustments prior to automatically transposing the grid-slide image to a bathythermograph aperture card. The complete routine operation, including the loading and positioning of the slide relative to the grid in the Processor, takes approximately 50 seconds.

Historical bathy-files can also be converted to the new system by simply replacing the present viewer-assembly with another modification unit. A variety of such units will allow for a wide range of applications in the field of oceanographic data retrieval, i.e. the storage of submarine photographs.

To take full advantage of the system, the peripheral equipment should include the following:

(1) an aperture card reproducer for making low-cost copies of the bathythermograph aperture card;

(2) an IBM key-punch for punching pertinent environmental data on the card;

(3) an IBM punch-card sorter for sorting the bathythermograph files;

(4) an aperture card "viewer-printer" which serves a dual role, first for making photographic prints from the bathythermograph aperture cards and secondly, when equipped with a high speed card-feed attachment, for fast sequential examination of the pre-sorted cards.

The Bathythermograph Card Processor is not necessarily confined to the laboratory, but can be considered as a sea-going microfilm device.

The principle of the system described in this paper has wide application in oceanography, but essentially offers an immediate solution to handling all forms of bathythermograph data. This is accomplished by introducing a new format for the storage of bathythermograph records which is compatible with current data retrieval technology. In doing so, it lends a new degree of sophistication to the bathythermograph, while at the same time preserving all the attributes of the original bathythermograph trace.

The author gratefully acknowledges the encouragement provided by Dr W. M. Cameron, the useful discussions with Mr F. G. Barber and the help of Dr N. J. Campbell in the preparation of this paper. He is especially grateful

[1]The camera used was a Filmsort-1000 d Processor-Camera, manufactured by the Minnesota Mining and Manufacturing Company.

[2]Canadian Government Specifications Board, Specification 72-GP-1A, Card Aperture, 35 mm Microfilming of Engineering and Architectural Drawings.

for the assistance provided by Messrs E. H. Bowler and A. B. Forward of the Division of Mechanical Engineering of the National Research Council of Canada for their part in the development of the modification unit to the camera. The co-operation of the Minnesota Mining and Manufacturing Company is also gratefully acknowledged.

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Further Evidence of Hardiness of "Silver" Pike

On August 26, 1962, a thin live "silver" pike (a variant of the northern pike, *Esox lucius*, described by Lawler (1960) was captured in a gill net set in shallow water of Heming Lake, Manitoba. The fish (38 cm long) was placed in a fish box with the remainder of the catch and brought back to the examination table about 15–20 min later. There was still some gill movement, even after this time, so it was placed in a retaining pen; after a while it appeared to be swimming satisfactorily.

On August 27, 1962, the pike was removed from the tank and was subjected to the routine measurements required for all fish captured. In addition to this, its small intestine was removed for parasitological examination. This procedure involves making an incision about 4 cm long in the abdomen, and then with a pair of scissors, cutting across the distal end of the stomach near the pyloric valve and the proximal end of the large intestine, thus leaving two unconnected portions of the alimentary tract. After this had been done to the pike, it lay on the examining table, moist because of recent rain, for about 20 min after

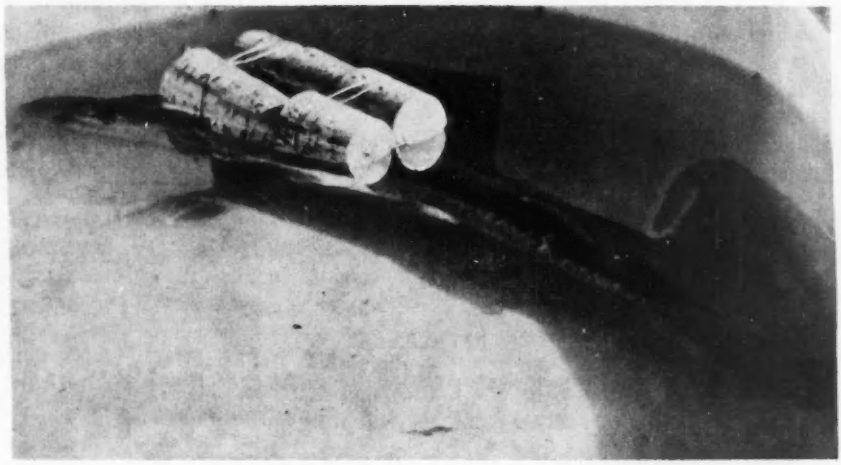

FIG. 1. "Silver" pike, *Esox lucius*, with cork floats to keep fish in upright position.

which a series of taxonomic measurements was taken. After completing these measurements, the writer noted that the gills were still moving and at this point the fish was once again placed in an aquarium where it floated to the bottom; however, the gill covers continued to open and close. The time was approximately 11.00 a.m. The fish was observed periodically during the day and by 5.00 p.m. a decision was made to suture the abdomen, as it was then swimming in an

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upright position. The fish was removed from the water and the cut ends of the alimentary tract tucked into the coelom; the abdomen was sutured with nylon thread and the fish was once again returned to water.

At 8.00 a.m. on the following day (August 28, 1962) the fish was still alive but lying on its side. At 2.00 p.m. that day it was still lying on its side, but respiratory movements were evident. To stabilize the fish's equilibrium, six small corks were fashioned into a float which was attached to the dorsal surface of the pike's body by a cradle of tantalum wire running around the pike's body. The float kept the fish in an upright position and it began to swim around the tank (Fig. 1). During the next few days, it continued to move about actively in the water. No serious attempt was made to feed this fish, as it was thought each day that it would only live a relatively short time. Without food, it continued to live in the aquarium with no obvious emaciation.

On September 12 (17 days later) the fish was transferred to a closed pen in the open lake. The corks were removed and it was able to maintain its equilibrium. The fish continued to live for approximately 2 more weeks before expiring on or about September 28.

More than 30 days had elapsed from the time the intestine was removed until the fish died. It is conceivable that the pike acquired some nourishment through absorption from the stomach of digested material. What is most striking about this pike was its ability, in spite of the lack of aseptic conditions and having undergone these traumatic experiences, to survive for such a long period of time. The apparent hardiness of silver pike was noted by Lawler (1960), and although the hypothesis that the mutant "silver" pike is hardier than the true northern pike has not been tested, accumulating circumstantial evidence tends to support the idea.

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Utilization of Lipids by Fish. III. Fatty Acid Oxidation by Various Tissues from Sockeye Salmon *(Oncorhynchus nerka)*

The enzymic oxidation of saturated fatty acids by preparations from muscular tissue of fish has been the object of previous studies of this series (Bilinski, 1963; Bilinski and Jonas, 1964) and the oxidation of fatty acids by fish liver has been studied by Brown and Tappel (1959). In the present study the fatty acid oxidizing ability of six different tissues from both juvenile and adult fish was compared. Data on the oxidation of acetate by various tissues were also obtained. These experiments were conducted with tissue slices and C^{14} labelled substrates.

Sockeye salmon (*Oncorhynchus nerka*) employed in the present study were held in fresh water aquaria in connection with other investigations at this laboratory (McBride *et al.*, 1963). Adult pre-spawned fish (1300–2000 g) were kept without feeding. Juvenile fish (50–100 g) were maintained on a pellet ration (J. R. Clark Co., Salt Lake City, Utah) and beef liver. The juvenile fish were not fed for about 20 hr prior to killing. Two adult and four juvenile fish were sacrified for experiments with each of the substrates, but only one adult fish was used with octanoate-1-C^{14}. The techniques employed for the incubation of tissue slices and for the estimation of the activity were the same as the ones used in previously reported experiments (Bilinski, 1963; Bilinski and Jonas, 1964).

The results of experiments conducted on oxidation of acetate, octanoate and myristate by various tissues from adult and juvenile sockeye salmon are presented in Tables I and II. Data on the formation of $C^{14}O_2$ from acetate-1-C^{14} show highest activity in kidney in both adult and juvenile salmon. Lower activity was found in liver, heart and lateral line muscle, whereas brain and dorsal muscle showed only a very limited ability to oxidize acetate. With octanoate-1-C^{14} as substrate in adult fish, liver, kidney, heart and lateral line muscle had similar activities while brain and dorsal muscle were considerably less active. In the oxidation of octanoate, the liver, and to a lesser extent other tissues, had a higher activity in juvenile than in adult fish. In fish at both stages of development the formation of $C^{14}O_2$ from myristate-1-C^{14} occurred most rapidly in the kidney, somewhat less rapidly in liver, heart and brain, slowly in lateral line muscle and very slowly in ordinary muscle. In most of the tissue the ability to oxidize myristate was more pronounced in the adult than the juvenile fish. Although in several tissues differences in activities between juvenile and adult fish were observed, the number of comparative experiments is not sufficient to draw any general conclusion in this respect. However the results do reveal a spectrum of activities in the various tissues which is very similar in juveniles and adults.

The rate of oxidation of labelled fatty acids by various tissues *in-vitro* has been the object of several investigations with mammals (see review by Fritz,

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TABLE I. Oxidative activity of various tissues from juvenile sockeye salmon.

Tissue	Substrate		
	Na-Acetate-1-C^{14}, 1 mM	K-Octanoate-1-C^{14}, 1 mM	K-Myristate-1-C^{14}, 0.1 mM
	Per cent radioactivity converted to $C^{14}O_2$ per mg protein N per hour		
Dorsal muscle	nil	nil	0.03
" "	"	"	0.06
" "	"	"	0.05
" "	"	<0.01	0.12
" "	"	<0.01	0.06
" "	"	<0.01	0.08
" average	**nil**	**<0.01**	**0.07**
Lateral line muscle	1.50	0.68	0.19
" " "	1.33	0.93	0.28
" " "		0.52	0.11
" " "		1.10	0.48
" " "		1.32	0.60
" " "			0.31
" " average	**1.42**	**0.91**	**0.33**
Heart	1.36	2.42	2.85
"	1.95	1.90	1.80
"	1.46	1.82	2.13
"	1.32	1.77	1.55
"		1.55	
" average	**1.52**	**1.89**	**2.08**
Liver	2.13	3.88	1.76
"	1.74	4.05	1.67
"	2.47	4.20	2.08
"	2.85	3.30	1.06
"	2.88	3.46	
"	2.95	3.32	
" average	**2.50**	**3.70**	**1.64**
Kidney	5.28	2.15	5.50
"	6.50	2.42	4.95
"	5.92	2.24	6.45
"	6.12	1.10	6.83
"	5.62	1.15	6.90
"	7.03	1.04	4.50
" average	**6.08**	**1.68**	**5.86**
Brain	0.23	0.14	1.02
"	0.24	0.06	1.52
"	0.29	0.11	1.32
"	0.26	0.09	2.04
"	0.24	0.06	1.38
"		0.08	
" average	**0.25**	**0.09**	**1.46**

TABLE II. Oxidative activity of various tissues from adult sockeye salmon.

Tissue	Substrate		
	Na-Acetate-1-C^{14}, 1 mM	K-Octanoate-1-C^{14}, 1 mM	K-Myristate-1-C^{14}, 0.1 mM
	Per cent radioactivity converted to $C^{14}O_2$ per mg protein N per hour		
Dorsal muscle	0.18	0.02	0.08
" "	0.12	0.03	0.04
" "	0.12	0.02	0.09
" "	0.08		0.06
" "	0.10		0.04
" "			0.08
" average	**0.12**	**0.02**	**0.07**
Lateral line muscle	1.20	0.67	0.66
" " "	1.00	0.80	1.12
" " "	1.05		0.52
" " "	1.17		0.49
" " "	1.43		
" " average	**1.17**	**0.73**	**0.70**
Heart	1.38	1.22	3.70
"	1.87	1.07	3.30
"	2.23	1.05	3.20
"			2.57
"			2.93
"			3.02
" average	**1.83**	**1.11**	**3.12**
Liver	1.93	0.83	4.85
"	1.76	1.60	3.95
"	2.14	1.24	2.87
"	1.13		4.05
"	1.26		3.30
"	1.19		3.05
" average	**1.57**	**1.22**	**3.68**
Kidney	5.76	1.13	4.10
"	5.92	1.26	6.05
"	5.84		6.77
"	6.25		7.70
"	6.74		5.60
"	5.80		7.75
" average	**6.05**	**1.20**	**6.33**
Brain	0.14	0.07	1.27
"	0.20	0.04	1.61
"	0.15	0.03	1.19
"	0.10		0.96
"	0.12		0.98
"			0.82
" average	**0.14**	**0.05**	**1.14**

1961) and the present findings are in general agreement with this earlier work with mammals. Thus in mammals the highest activity occurs in liver, heart and kidney, while the brain and skeletal muscle have lower activity.

In confirmation of observations made earlier with rainbow trout (Bilinski, 1963) it was found that in salmon the fatty acid oxidizing complex is more active in the lateral line muscle than in the ordinary muscle. It appears also that the lateral line muscle has a very pronounced ability to metabolise acetate, showing in this respect an activity similar to that of liver and heart. It seems clear that in fish there is a basic difference between the lateral line and ordinary muscle in their capacity for oxidative metabolism of fatty acids and acetate. This view is consistent with the fact that succinic dehydrogenase was found to be more active in the lateral line than in the ordinary muscle of fish (Unemura, 1951 a, b; Fakuda, 1958). An indication that lipids are utilized to a larger extent in the lateral line muscle of fish than in the ordinary muscle was also obtained by George (1962) in a study of mackerel. He found that the lateral line muscle had a higher lipase activity than the ordinary muscle and histochemical examination of these muscles showed that succinic dehydrogenase was localized in mitochondria which were numerous in the red fibres from lateral line muscle and sparse in the white fibres from the ordinary muscle.

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An Unusually Late-Spawning British Columbia Chum Salmon

On April 9, 1962, Mr C. Cook saw a large salmon in the shallow estuarial waters of a small creek at Deep Bay on the east coast of Vancouver Island. The fish was brought to the attention of Messrs W. Caulfield and H. Neate of this Station's staff, who recognized it as an unusually late-spawning male chum salmon (*Oncorhynchus keta* (Walbaum)) and brought it to the author for further examination.

It was a typical fresh stream-run fish. The skin was darkened but the scales were loose and not resorbed. The flesh was firm and milt was easily expressed. The weight was 9.8 lb (4.4 kg) and the fork length 32 inches (81.3 cm). Scale reading showed that the fish was in its fifth year.

Fence counts made on the stream from 1960 to 1963 indicate that small numbers of chum salmon migrate into the stream from mid October to early December. The latest spawning along the southeast coast of Vancouver Island, of which the author is aware, was in February, in the Nanaimo River, 45 miles southeast of Deep Bay.

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